

CONTRIBUTIONS TO PALÆONTOLOGY
—
STUDIES ON CENOZOIC VERTEBRATES
OF
WESTERN NORTH AMERICA
—

WILSON, SCHULTZ, HOWARD, COLBERT
LAUDERMILK AND MUNZ

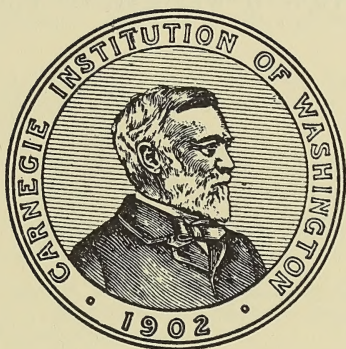
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OF WESTERN NORTH AMERICA

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- II. WILSON, ROBERT W. Pliocene Rodents of Western North America. Pages 21 to 73 and 2 text-figures. (Issued July 1937)
- III. SCHULTZ, JOHN R. A Late Cenozoic Vertebrate Fauna from the Coso Mountains, Inyo County, California. Pages 75 to 109, 8 plates and 5 text-figures. (Issued September 1937)
- IV. SCHULTZ, JOHN R. A Late Quaternary Mammal Fauna from the Tar Seeps of McKittrick, California. Pages 111 to 215, 17 plates and 12 text-figures. (Issued July 1938)
- V. HOWARD, HILDEGARDE. The Rancho La Brea Caracara: A New Species. Pages 217 to 240, 3 plates and 1 chart. (Issued July 1938)
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CONTRIBUTIONS TO PALÆONTOLOGY

I

NEW MIDDLE PLIOCENE RODENT AND LAGOMORPH
FAUNAS FROM OREGON AND CALIFORNIA

By ROBERT W. WILSON

With three plates

[Issued June 30, 1937]

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NEW MIDDLE PLIOCENE RODENT AND LAGOMORPH FAUNAS FROM OREGON AND CALIFORNIA

INTRODUCTION

The purpose of this paper is the description of two rodent faunas in the collections of the California Institute of Technology. Although coming from widely separated areas, these assemblages are of approximately the same age. The first fauna to be discussed is that from Pliocene strata near Rome, Malheur County, Oregon. It exhibits some diversity of type although the associated larger mammals are known by very fragmentary remains. The second rodent fauna comes from the Kern River deposits, San Joaquin Valley, California. The Kern River rodents and lagomorphs, and the larger mammals found with them, share with other Tertiary assemblages of the San Joaquin Valley the important task of determining the time relationships between the nonmarine deposits in which they are found and the standard marine sections of the Pacific Coast.

The illustrations for this paper are from photographs by the late H. Wm. Menke, and have been carefully retouched and arranged into plates by John L. Ridgway.

ROME FAUNA

The Rome fauna occurs in lake beds exposed along the Crooked Creek drainage, tributary to the Owyhee River, five miles southwest of Rome, Malheur County, Oregon. Locally, in the fossiliferous area, the section consists of light green to white tuffaceous sandstones, pebble beds, and mudstones. Most of the fossils were obtained from a narrow band of sediments situated near the base of the section as exposed along the eastern side of Dry Creek, a small tributary of Crooked Creek. Except for an isolated cheek-tooth of *Castor*?, the entire rodent fauna was obtained from this limited stratigraphic zone.

The following rodent and lagomorph types have been recorded from the Rome fauna:

Rodentia

Mylagaulus? cf. *monodon* Cope

Dipoides stirtoni Wilson

Castor? sp.

Goniodontomys disjunctus n. gen. and sp.

Lagomorpha

Hypolagus vetus (Kellogg)

Hypolagus sp.

Associated with the above assemblage are rather fragmentary mammalian remains representing a diverse fauna. These remains have not been studied in detail, but the following forms have been recognized in the fauna:

<i>Scapanus(?)</i> sp.	Felid large sp.
<i>Plihippus</i> near <i>spectans</i> (Cope)	Felid small sp. (possibly <i>Machærodont</i>)
<i>Teleoceras fossiger?</i> (Cope)	Camelid large sp.
<i>Prosthennops</i> sp.	Camelid small sp.
<i>Sphenophalos nevadanus</i> Merriam	Cervid sp.
<i>Lutra</i> sp.	Mastodont sp.
<i>Plionictis</i> near <i>ogygia</i> (Matthew)	Turtle, fish, reptile, and bird remains
<i>Lutravus</i> cf. <i>halli</i> Furlong	
? <i>Ælurodon</i> sp.	
Canid (in <i>Ælurodon-Osteoborus</i> group) probably n. gen.	

Work on the Rome fauna has not been intensive enough to determine the exact time relations of the assemblage. However, a middle Pliocene age or a stage of evolution comparable to that represented by the Rattlesnake-Thousand Creek faunas seems certain. More particularly, the Rome rodent fauna suggests by the presence of *Castor?* and of a vole that it is at least as advanced as the Thousand Creek fauna.

The presence, in the Rome assemblage, of a mole, beavers, an otter, and fish remains points to a rather moist environment with bodies of water in the immediate vicinity. The limited collecting area, the lithology of the sediments, and the large number of specimens of *Dipoides* suggest that the deposits are lacustrine in origin.

SYSTEMATIC DESCRIPTION OF FAUNA

RODENTIA

Mylagaulidæ

The Mylagaulidæ present many problems which need to be solved before a satisfactory understanding of the group is reached. Not only are the various species in considerable confusion, but even the genera are in an uncertain state of definition. The relation of horned to hornless types has not been determined, nor have the limits of individual and age variation been fixed.

It has been suggested that the presence or absence of horns is a sex character. However, as Matthew has pointed out, no other known rodent possesses a like amount of sex distinction, although, as he states further, this argument is partly vitiated by the fact that no other rodent possesses horns. Such a variation, in a burrowing form in which the horns were presumably used as digging implements, would

place the female at a decided disadvantage. Moreover, the California Institute of Technology collections embrace a number of Miocene and Pliocene mylagaulids complete enough to demonstrate the presence of horns if such structures were actually present. However, no horns were noted, and it is extremely unlikely that all these skulls and similar specimens found elsewhere represent females. Judging from published descriptions, horned types are everywhere relatively rare.

It can be shown rather satisfactorily that the tooth-pattern undergoes considerable change during the life of the individual. The variation in the skull is not known, nor is there a suitable answer to the question of individual variation in premolar pattern. In certain species the individual variation of teeth representing approximately the same stage of wear is not great. However, if the conclusion implied by this statement is applied widely, an extremely large number of species in proportion to the number of known specimens would have to be recorded. Moreover, some of the mylagaulid material in the Institute collections points to considerable individual variation in specimens from the same zone and locality.

By means of relatively unworn teeth it is possible to demonstrate in the upper premolar the derivation of the lakes from the original basins in the unworn teeth and, moreover, the origin of certain dental areas from particular cusps, exactly as this has been done in the cheek-teeth of such forms as *Equus*. The lower premolar appears susceptible to a similar treatment, although greater difficulty is encountered in tracing the derivation of the adult pattern than in the upper premolar. Use of this method of study leads to a clearer appreciation of the differences or similarities in two distinct species than can be obtained by citing the number of lakes present and their arrangement in varying numbers of rows. It is felt that this method of study combined with sectioning of individual teeth might eventually lead to an understanding of the characters exhibited by isolated grinding teeth. Such work would have to be based primarily on a thorough study of species which are known by a large number of specimens and in which teeth in all stages of wear are present.

Doubtless a greater number of species and perhaps genera are in existence than have been described. It is conceivable that such eminently burrowing types might have a rather limited geographic range and that consequently a number of distinct species might be present in each faunal stage. However, with our present understanding of the group, the establishment of more types is decidedly not a desirable procedure.

Pliocene mylagaulids are known only by fragmentary material. A possible exception is *Epigaulus hatcheri*, the type of which consists

of a fairly complete skull and skeleton. Gidley referred the beds (Republican River) from which the type was obtained to the upper Miocene. The type locality is near Long Island, Kansas. Stirton¹ has recently referred a fauna, termed by him the Long Island fauna, to the middle Pliocene. *Mylogaulus monodon* and *M. sesquipedalis* also have been recorded from Pliocene beds. The type localities of these two species are in the Republican River beds, and hence the exact age of the specimens is not known, although they are usually referred to the lower Pliocene. A referred specimen of *M. monodon* apparently comes from the same beds as *E. hatcheri*. Matthew has suggested that *M. monodon* may have to be referred to *Epigaulus* and states that *M. monodon* and *E. hatcheri* are probably identical.² However, Matthew in describing the type of *M. monodon* states that P $\bar{4}$ has no cement outside the external enamel ring. The type of *E. hatcheri*, as described by Gidley, possesses premolars in which an investment of cement forms a functional part of the teeth. This discrepancy can be removed only by assuming: (1) that cement was present originally on the type of *M. monodon* and has dropped away; (2) that the type was incorrectly described (not probable); or (3) that the presence or absence of cement is not a distinctive character. Perhaps the explanation given under (1) is the most likely. *M. sesquipedalis* is distinguished from *M. monodon* by its smaller size, fewer, less elongate lakes, and more irregular arrangement of lakes.

Mylogaulus? cf. monodon Cope

Pliocene mylogaulids from the Great Basin have been known hitherto only by two isolated grinders. A P $\bar{4}$ has been recorded by Miss Kellogg³ from Thousand Creek, Nevada, and E. Raymond Hall has described a lower premolar from the Fish Lake Valley beds of Nevada.⁴ In comparison, mylogaulid material from Rome is relatively abundant. The most perfectly preserved specimen is an almost complete lower jaw, C.I.T. No. 72 (Plate 1, figs. 8, 8a, 8b). The extreme tip of the coronoid is missing, as is the posterior portion of the angle, but the dentition is complete including all three molars. A second ramus, No. 1951, which was also obtained is more fragmentary than No. 72. The dentition in this specimen lacks M $\bar{1}$. Isolated premolars, Nos. 1952-1958 (Plate 1, figs. 1-7), both upper and lower, and various fragmentary limb elements are present also in the Rome collection. The two rami represent young individuals in which practically none of the enamel inflections has become isolated, thus making comparisons with other specimens difficult. All the remains have been considered as representing a single species, although this is a doubtful procedure with reference to one or two specimens.

The Rome species is characterized by premolar teeth which become elongate in a fore-and-aft direction with wear. The enamel lakes are

¹ R. A. Stirton, Univ. Calif. Pub., Bull. Dept. Geol. Sci., vol. 23, no. 8, 284, table 3, 1934.

² W. D. Matthew, Bull. Amer. Mus. Nat. Hist., vol. 50, art. 2, 75, 1924.

³ L. Kellogg, Univ. Calif. Pub., Bull. Dept. Geol., vol. 5, no. 29, 429, fig. 10, 1910.

⁴ E. R. Hall, Univ. Calif. Pub., Bull. Dept. Geol. Sci., vol. 19, no. 12, 307-308, figs. 18-19, 1930.

numerous, elongate, and tend to arrange themselves in rows. The teeth possess an external investment of cement which in some specimens at least is a functional part of the tooth. The ramus is very heavy and deep, thick transversely below the premolar. P4 possesses from six to usually nine lakes. The single specimen exhibiting six lakes, No. 1954 (Plate 1, fig. 2), is relatively unworn and indicates that an increase in the number of lakes takes place with further wear. The lower premolars possess a minimum of eight lakes in a well-worn tooth and a maximum of nine, although this figure might be increased to ten. The teeth are larger than those of *Mylogaulus laevis* but smaller than in the type of *Epigaulus hatcheri*. A mylagaulid humerus is distinctly smaller than the comparable element in *E. hatcheri*.

The Rome species does not agree exactly with any described species, but may be closest to *M. monodon*. Compared with the type of *M. monodon*, the Rome species possesses a larger ramus, which is deeper and more distinctly bulged by the premolar. P4 is narrower transversely and possesses a larger number of lakes. The latter show a somewhat different arrangement. A P4 referred by Cope to *M. monodon* agrees in size and shape with the Oregon type but the occlusal pattern appears to be distinct. If both the type and referred specimen of *M. monodon* are actually conspecific, the Rome specimens are rather close to them. However, cement forms a functional part of the wearing surface of the premolar, a character in which they differ from *M. monodon* as described by Matthew.

Epigaulus hatcheri Gidley,¹ although with larger P4/4, resembles the type from Rome in the presence of an external coat of cement on the cheek-teeth. The ramus of the Rome species apparently possesses slightly different proportions, but is thick and deep below P4, a character seen in *E. hatcheri*. The tooth-row is slightly shorter in the Oregon form, and P4/4 differ somewhat in pattern in the two species. If *E. hatcheri* and *M. monodon* are conspecific, the type from Rome would be close to that species. However, the upper premolars of the Oregon type show a close agreement with those of a species of mylagaulid from Bartlett Mountain, Oregon (Pliocene). A very well-preserved skull of the latter is without bony horn-cores, a character in which it differs distinctly from *Epigaulus*.

Mylogaulus species from Fish Lake Valley, Nevada, is represented by a single isolated P4. This species is smaller than the Rome type with somewhat different occlusal pattern. Unfortunately, the dimensions of the figures given by Hall do not agree very well with his measurements. In any case the species is probably distinct from that found at Rome.

The only other Pliocene mylagaulid material on record from the Great Basin is an unworn P4 from the Thousand Creek beds, described by Miss Kellogg. This specimen was referred by her to *M. monodon*. Although Miss Kellogg compared this tooth directly with figures of the type of *M. laevis* Matthew in the belief that the latter was still referred to *M. monodon* Cope, the Thousand Creek form is probably closer to Cope's species than to *M. laevis*. However, in the case of the Virgin Valley specimen, referred by Miss Kellogg to *M. monodon*, the figure shows a tooth more closely resembling *M. cf. laevis* from Skull Spring than *M. monodon*. U.C. No. 12580, a P4 referred to *M. pristinus*, may also represent the Skull Spring species. Virgin Valley mylagaulids in the California Institute collection indicate the presence of a species distinct from the Skull Spring type. Whether this second

¹ J. W. Gidley, Proc. U. S. Nat. Mus., vol. 32, no. 1554, 627-636, pls. 58-65, 1907.

species is referable to *M. pristinus* was not determined. An isolated P4 in the Institute collection from Thousand Creek appears to be distinct from the Rome species.

The fragmentary limb material from Rome is too incomplete to add anything to our knowledge of the skeletal structure of the Mylagaulidæ.

It is quite possible that *Mylagaulus?* cf. *monodon* from Rome represents an undescribed species of rodent. In view of our very incomplete knowledge of the Mylagaulidæ nothing would be gained by establishing a new species.

Measurements (in millimeters) of Mylagaulus? cf. monodon Cope

	No. 72	No. 1951
P4-M3, alveolar length	19.1	17.8
Length of diastema, I-P4.....	10.6	...
Depth of ramus beneath P4.....	18.9	...
Depth of ramus beneath diastema.....	12.6	...
Thickness (transverse) of ramus beneath P4.....	11.8	...
	Maximum	Minimum
Several isolated P4's:		
Greatest antero-posterior diameter.....	12.0	11.0
Greatest transverse diameter.....	6.4	5.6
Several isolated P4's:		
Greatest antero-posterior diameter.....	13.3	10.4
Greatest transverse diameter.....	6.0	5.2

Castoridæ

Dipoides stirtoni Wilson

Remains of this species of aberrant beaver are very common in the Rome fauna. A detailed account of the fossil material has already been published.¹

Castor? sp.

The true beaver is represented by a single isolated M2?. This specimen, No. 1961 (Plate 1, figs. 9, 9a), represents an individual comparable in size to the existing *Castor canadensis*. The base of the tooth is somewhat damaged, but practically the full height of the cheek-tooth seems to be preserved. Three internal and one external lateral grooves are present, as is normal for *Castor*. The external groove extends to the base of the portion preserved, while the three internal inflections extend somewhat less than half the distance to the base of the tooth. In a measure, the extent of the internal grooves is a function of the amount of wear the tooth has undergone, but undoubtedly the grooves are much less persistent than in Recent species. The posterior groove (metastrid) is slightly longer than the other two (mesostrid and parastrid), which are equal in length. The occlusal pattern is that of a normal *Castor* except for the presence of an enamel lake in the anterior enamel loop. Such a lake is present in the first molar of a ramus of the Asiatic *C. andersonni*, as figured by Schlosser.² However, in this species M1 and M2 are shorter transversely than is the Rome molar, although M2 has the same antero-posterior diameter, and M1 only a slightly greater measurement. *C. andersonni*, together with the Asiatic species *zdanskyi* and *broilii*, has been placed by Young in a new genus *Sinocastor*. The

¹ R. W. Wilson, Carnegie Inst. Wash. Pub. No. 453, pt. 3, 1934.

² M. Schlosser, Palæ. Sin., ser. C, vol. 1, fasc. 1, pl. 2, fig. 43, 1924.

present author has not observed the above-mentioned lake in any other specimens of *Castor*.

There may be some doubt as to the association of the Rome *Castor*? with the rest of the rodent fauna. The occurrence of the specimen in an area isolated from that in which the other rodents were obtained, and the presence of beds of possible upper Pliocene or Pleistocene age in the vicinity, raise this question. However, not only does the association in the field of *Castor*? with *Pliohippus* teeth obviate this possibility to a large extent, but the characters exhibited by the specimen itself point in the same direction.

True beavers from North America are extremely rare in beds older than the upper Pliocene. Two teeth from the upper Snake Creek (P4 and P4) and the present one are all that have been so far recorded. The geologic range of *Castor* is not accurately determined, but the genus or closely allied types are known from the early Pliocene of Europe and Asia.

Measurements (in millimeters) of Castor? sp.*

M2?, antero-posterior diameter.....	8.2
M2?, transverse diameter.....	7.1

* Measured at occlusal surface.

Microtinæ?

Goniodontomys disjunctus n. gen. and sp.

Geological Age and Locality—Middle Pliocene beds exposed along the Crooked Creek drainage, tributary to the Owyhee River, five miles southwest of Rome, Malheur County, Oregon.

Genotype—No. 1959, C.I.T. Coll. Vert. Pale., an incomplete left ramus bearing M1–M2 (Plate 2, figs. 2, 2a, 2b).

Referred Specimen—No. 1960, C.I.T. Coll. Vert. Pale., a small fragment of ramus with left M2 in place.

GENERIC AND SPECIFIC CHARACTERS

Mandibular incisor passing from lingual to buccal side of tooth-row, and probably extending well up into the ascending ramus. Cheek-teeth hypsodont, prismatic, and flat-crowned, rooted and without cement. Re-entrant angles of cheek-teeth generally opposed. Re-entrant angles from opposite sides normally in contact. Enamel not differentiated into thick and thin tracts. M1 with posterior loop, three triangles, and complex anterior loop. Second external salient angle of M1 opposite third internal salient angle.¹ Ramus heavy and apparently shortened. Length of tooth-row approximately as in *Mimomys primus*.

DESCRIPTION

Inferior Dentition—The mandibular incisor crosses from lingual to buccal side of the tooth-row under (?) M3, and probably extends well up into the ascending ramus. The first molar (Plate 2, fig. 2) is composed of a pos-

¹The system used by M. A. C. Hinton for enumeration of the re-entrant and salient angles has been adopted in this paper. See Hinton, *Monograph of the Voles and Lemmings (Microtinæ) Living and Extinct*, vol. 1, 22, 1926. To quote from Hinton: "In describing the teeth it is customary to enumerate the salient angles and re-entrant folds from before backwards in upper molars, and from behind forwards in lower molars, the first salient angles on each side being formed by the transverse loop."

terior loop, three triangles, the anterior two opposed to form a somewhat tetragonal loop of enamel, and a complex anterior loop. The anterior loop is complicated by a pronounced inflection on the internal side, a similar but less pronounced inflection buccally, and an antero-median inflection in front. A very shallow fold of enamel is also present on the buccal side and just anterior to the main external fold mentioned above. The posterior triangle communicates broadly with the posterior loop, but the commissures connecting the median pair of triangles with the anterior and posterior portions of the tooth are narrow. $M\bar{2}$ is a less complex tooth which may be characterized as possessing three loops of enamel connected by narrow commissures. The median loop is apparently analogous to the two posterior alternating triangles in normal voles. A second, less worn specimen of *Goniodontomys*, No. 1960, possesses slightly more triangular salient angles, and in addition some slight angulation of the anterior loop suggestive of the two more or less alternating triangles which replace this loop in the normal vole dentition. $M\bar{2}$ is distinctly shorter than $M\bar{1}$.

Ramus—The ramus (Plate 2, figs. 2a, 2b) is rather deep and is apparently shortened. The juncture of ascending and alveolar portions of the ramus occurs opposite the posterior root of $M\bar{1}$ as in voles, rather than opposite the posterior root of $M\bar{2}$ as in *Neotoma*. The ridge for attachment of the masseter muscle terminates anteriorly about opposite the posterior surface of the anterior root of $M\bar{1}$. The masseter medialis scar is slightly less developed than the preserved portion of the masseter lateralis scar. The mental foramen is situated close to the superior surface of the ramus, and almost directly beneath the anterior tip of $M\bar{1}$. A second small foramen is found just above the tip of the ridge for the attachment of the masseter muscle. The area for symphyseal attachment extends back well under the posterior portion of $M\bar{1}$. In this character our genus resembles *Microtus* and differs from *Neotoma*. In the latter genus the symphyseal area is much more limited posteriorly.

RELATIONSHIPS

Although the systematic position of *Goniodontomys* is not entirely clear, it has been assigned to the Microtinæ. The genus is known by such fragmentary material that it is difficult to eliminate from consideration some other groups of rodents with hypsodont teeth. *Goniodontomys* is widely separated from most microtines by the more or less complete opposition of the usually alternating prisms of the cheek-teeth. The second molar has an occlusal pattern somewhat like that exhibited by some species of *Hyperacrius* and *Eothenomys*. The first molar, however, is quite unlike the usual microtine $M\bar{1}$, especially in the nearly opposite second external and third internal salient angles. In voles of more normal type, when the triangles are opposite one another, the second external triangle or salient angle is opposed by the second internal triangle. An approach to the pattern of $M\bar{1}$ in the Oregon genus is made in a specimen of *Prometheomys schaposchnikowi*,¹ figured by Hinton, but the resemblance is remote. Moreover, the anterior termination of $M\bar{2}$ in *Goniodontomys* is not angular, as is usually the case in Microtinæ. No. 1960, the dentition of which is somewhat less worn than the type, suggests this angular termination, and some Recent voles possess second molars with a more or less rounded appearance.

¹ M. A. C. Hinton, *Monograph of the Voles and Lemmings*, vol. 1. Brit. Mus. Nat. Hist., 86, fig. 55, 1926.

Relationship to the microtines is suggested in *Goniodontomys* by the thin enamel of the cheek-teeth, the triangular shape of the salient angles, the relatively large number of elements comprising $M\bar{1}$, and various characters in the ramus. If the intermediate-external triangle of $M\bar{2}$ and the internal triangles of $M\bar{1}$ of *Goniodontomys* were shifted anteriorly, an occlusal pattern would result quite close to that in many microtines.

If *Goniodontomys* is to be assigned to the Microtinæ, the genus is a vole and not a lemming. Enough of the mandibular incisor is preserved in the type specimen to demonstrate this conclusion.

Reference of *Goniodontomys* to some group of rodents other than the microtines seems less likely than the present assignment. A number of rodent families possess members with hypsodont teeth, but most of them are quite removed structurally as well as geographically from the Oregon genus. *Neotoma* and its relatives suggest a relationship with *Goniodontomys* in certain features of the dentition. However, the dentition of *Neotoma* has relatively thick enamel borders, the salient angles are less triangular, the ramus is slimmer, and the ascending ramus rises from the horizontal ramus farther back than in *Goniodontomys*. Moreover, not only does *Goniodontomys* possess a more complicated $M\bar{1}$, but it is hardly likely that any *Neotoma*-like form from the middle Pliocene would be so high-crowned as is the case in the former genus. The second lower molar of *Neotoma* is strikingly like that of *Goniodontomys* in the general aspect of the pattern. On the other hand, in our genus the second external salient angle and the third internal salient of $M\bar{1}$ form a loop directed forward and inward. The corresponding loop in *Neotoma* is more transverse or, if oblique, is directed slightly forward and outward. A fossil species of *Oxymycterus*, *impexus* Ameghino from the Pampean of South America, resembles *Goniodontomys* more closely in pattern of $M\bar{1}$ than does *Neotoma*. However, $M\bar{2}$ is quite different and the resemblance is probably superficial.¹

The cape-rats possess extremely hypsodont teeth with occlusal patterns quite similar to that of microtines. However, the group has never been recorded from North America and its dental pattern resembles that of *Goniodontomys* less than does that of some voles. Moreover, early Pliocene forms are known from Asia, and these are no closer to our genus in occlusal pattern than are existing types. The early Pliocene Asiatic specimens show a pronounced tendency to isolate the re-entrant folds of enamel as lakes. In this respect *Goniodontomys* is closer to normal microtines, in which such a condition is limited to extreme wear.

Other groups of rodents with hypsodont teeth have decidedly less resemblance to *Goniodontomys* than do those mentioned above. Such forms as *Sigmodon*, the jerboas, and the Gerbillinæ differ in one or more major characters.

If *Goniodontomys* is a vole, it is the oldest so far recorded. Unfortunately, it is not very close to existing forms, and apparently represents an aberrant type. It is surprising that the Microtinæ are not more common in the Tertiary, as the subfamily must have had a considerable geologic range. *Poamys* Matthew from the lower Snake Creek was regarded by Matthew as possibly a structural ancestor of the Microtinæ. The validity of this hypothesis cannot be determined on available evidence. However, the presence of *Goniodontomys* and *Poamys* in beds older than the upper Pliocene sug-

¹ F. Ameghino, Contr. al Conocimiento de los Mam. Fos. de la Republ. Argent., Actos Acad. Nac. de Ciencias Republ. Argent. en Cordoba, Atlas, pl. 4, fig. 3b, 1889.

gests the possible presence of other microtine-like forms in the late Miocene and early Pliocene.

Since *Goniodontomys* is an aberrant type, it does not furnish much evidence as to the evolution of the Microtinæ. The opposition of the triangles in this genus does not necessarily demonstrate that this is the primitive microtine condition, although the perfect alternation of prisms seen in many voles is probably a specialized and advanced character.

Measurements (in millimeters) of Goniodontomys disjunctus n. gen. and sp.

C.I.T. No. 1959 (genotype). Middle Pliocene, Rome, Oregon

Length of crown, M1-M2.....	5.5
M1, antero-posterior diameter.....	3.0
M1, transverse diameter.....	1.5+
M2, antero-posterior diameter.....	2.2
M2, transverse diameter.....	1.5
Depth of ramus beneath M1.....	6.3

LAGOMORPHA

Leporidae

Hypolagus vetus (Kellogg)

Several fragmentary lower jaws and a number of isolated teeth, both uppers and lowers, appear to be referable to *Hypolagus vetus* (Kellogg).¹ The Rome specimens are of approximately the same size as topotype material of *H. vetus* from Thousand Creek. Characters exhibited by P3 agree with those of the latter material except that this tooth in the Rome form may be slightly broader on the average, with flatter or more gently rounded anterior face, which serves to widen this portion of the tooth. Some topotype specimens exhibit these characters, but the average specimen is probably somewhat different. The lower molariform teeth, as seen in No. 1962 (Plate 2, figs. 3, 3a), fragmentary left ramus with P3-M1, and No. 1963, fragmentary left ramus with P3-M1, C.I.T. Coll. Vert. Pale. from Rome, may be slightly larger than comparable material from Thousand Creek.

A single isolated P2 is present in our collections. If this tooth is referable to the same species as the rami, it differs from the Thousand Creek *H. vetus* in a lengthening of the tooth transversely. However, the specimen shows a deep antero-internal fold and a shallower antero-external fold as in *H. vetus*. The upper molariform teeth do not seem to show such heavy external ribs as in the Nevadan species.

C. L. Gazin has referred a large species of *Hypolagus* from Hagerman to *H. near vetus*.² In shape of P3 and in size of some specimens at least, the Rome material is close to that from Hagerman. If the Rome fauna is actually advanced over that from Thousand Creek, as is perhaps suggested by the presence of *Castor?*, the Thousand Creek, Rome, and Hagerman specimens may form a progressive series. However, it is doubtful if the Rome fauna as a whole is more advanced than that from Thousand Creek.

Compared with other known species of *Hypolagus*, the Rome specimens are readily distinguished by their large size as well as by characters in the dentition.

¹ L. Kellogg, Univ. Calif. Pub., Bull. Dept. Geol., vol. 5, no. 29, 436-437, fig. 20, 1910; L. R. Dice, Univ. Calif. Pub., Bull. Dept. Geol., vol. 10, no. 12, 181-182, figs. 4-5, 1917.

² C. L. Gazin, Proc. U. S. Nat. Mus., vol. 83, no. 2976, 112-114, fig. 1, 1934.

A large series of topotype material of *H. vetus* was available for comparison. It should be noted that this material shows decided variation in the characters of P3 as well as some variation in most of the other characters that have been used to establish species of *Hypolagus*. The Rome material is too scanty to permit one to say that the specimens average differently from those from Thousand Creek, although study of the collection suggests this to a certain extent. However, since certain specimens from Thousand Creek are closely comparable to individuals from the Oregon locality, the specific designation is justified.

Measurements (in millimeters) of Hypolagus vetus (Kellogg)

	No. 1962	No. 1963
P3-MI, occlusal length.....	9.1	9.3
Depth of ramus below MI, measured on inside.....	12.7	..

Hypolagus sp.

A left ramus of *Hypolagus* with P4-M3, No. 1964 (Plate 2, figs. 1, 1a), appears to represent a species distinct from *H. vetus*. This specimen is characterized by a much lighter dentition than is present in *H. vetus*, although the ramus is as deep and apparently as robust. The lower molari-form teeth have convex postero-internal ribs, most noticeably developed in P4 and M1. This surface is flattened in typical *H. vetus*. *H. vetus* from Rome may be intermediate in this respect. Several additional specimens representing individuals smaller than those of *H. vetus* in the collection have also been referred tentatively to this type. One isolated P3 is present which is smaller than the comparable tooth of *H. vetus*. Aside from difference in size, the tooth is close to the *vetus* type.

Comparison of the Rome species with small species of *Hypolagus* is handicapped by lack of suitable material. However, the robust jaw of the Rome form would seem to distinguish this species from others in which the dentition is similar in size.

It should be stated that sufficient material is not available to obviate the possibility that this second species of *Hypolagus* represents merely a young or immature stage of *H. vetus*. Comparisons, as stated above, are based mostly on a single ramus. A second jaw apparently possesses a larger dentition, but this is still distinctly smaller than that in *H. vetus* from Rome. Until more material becomes available it seems desirable to recognize two types from the Rome locality.

Measurements (in millimeters) of Hypolagus sp.

	No. 1964
P4-M3, occlusal length.....	8.4
Depth of ramus below M1, measured on inside.....	12.9

KERN RIVER FAUNA

The Kern River deposits are located about nine miles northeast of Bakersfield, in Kern County, California. A middle Pliocene rodent and lagomorph fauna obtained from these beds consists of the following forms:

Rodentia

Citellus? sp.

Peromyscus pliocenicus n. sp.

Lagomorpha

Hypolagus near *limnetus* Gazin

Hypolagus small sp.

SYSTEMATIC DESCRIPTION OF FAUNA

RODENTIA

Sciuridæ

Citellus? sp.

Sciurid remains from the Kern River beds are limited to a right ramus with P4-M2 and an alveolus for M3, No. 1965 (Plate 3, figs. 1, 1a); a second right ramus without dentition; and fragments of an upper and a lower incisor which may be referable also to this family. Specimen No. 1965 is the basis for the doubtful generic determination given above.

The dentition of No. 1965 is extremely worn and part of the first molar is missing. As a consequence, comparisons are difficult to make. No. 1965 is relatively small, agreeing in size with Recent specimens of *Callospermophilus lateralis certus*. The molars do not show the pronounced fore-and-aft compression and the high trigonids characteristic of typical *Citellus*, and the specimen certainly does not represent the genus in the restricted sense. P4 is rather triangular in outline and the anterior two cusps were probably closely appressed in their originally unworn condition. The mandibular incisor is relatively broad and lacks pronounced furrows. Thus, No. 1965 appears to represent the genus *Citellus* in a broad way, and to be related to such genera or subgenera as *Callospermophilus* and *Otospermophilus*, which occupy a position intermediate between typical *Citellus* and typical *Sciurus*.

No. 1965 seems to be more closely related to *Otospermophilus gidleyi* (Rattlesnake), *Citellus* sp. (Thousand Creek), and *Citellus?* sp. (Smiths Valley) than to any other Pliocene sciurids. It is about the size of these species and moreover agrees in general character of the dentition, at least in so far as may be observed in the well-worn dentition of the Kern River specimen.

Otospermophilus gidleyi Merriam, Stock, and Moody¹ from the Rattlesnake formation of eastern Oregon approximates the Kern River species in length of tooth-row, but the ramus of the former is deeper. The talonid rim in M2 of No. 1965 may be more angulate than in the Oregon species. Degree of angulation in No. 1965 is difficult to determine because of breaking away of the inner margins of the molars in the specimen. *Citellus?* sp.² from Smiths Valley, central Nevada, also approaches No. 1965 in size, although the tooth-row in the Smiths Valley species may be slightly longer. M2 of the former is slightly larger than the comparable tooth in the latter and may be somewhat more compressed antero-posteriorly. In addition, the mandibular incisor of the Nevadan species is heavier and perhaps slightly more compressed, although degree of compression is difficult to determine accurately with the present material. *Citellus* sp.³ from the Thousand Creek beds of northern Nevada is too inadequately known to permit comparisons. No. 1965 agrees with the Thousand Creek specimen in size. Other Pliocene Sciuridæ appear to be clearly distinguishable from the Kern River species.

For purposes of comparison it may be stated that the alveolar length, P4-M3, in No. 1965 is 8.4 millimeters.

¹ J. C. Merriam, C. Stock, and C. L. Moody, Carnegie Inst. Wash. Pub. No. 347, pt. 3, 68-69, fig. 23, 1925.

² R. W. Wilson, Carnegie Inst. Wash. Pub. No. 473, pt. 2, 19-20, pl. 1, fig. 5, 1936.

³ L. Kellogg, Univ. Calif. Pub., Bull. Dept. Geol., vol. 5, no. 29, 427-428, fig. 8, 1910.

Cricetidae

Peromyscus pliogenicus n. sp.

Type—Fragmentary right ramus with M $\bar{1}$ –M $\bar{2}$, No. 1966, C.I.T. Coll. Vert. Pale. (Plate 3, figs. 2, 2a).

Paratypes—Fragmentary left ramus with M $\bar{1}$ –M $\bar{2}$ and alveolus for M $\bar{3}$, No. 1967 (Plate 3, fig. 4); fragment of right maxillary with M $\bar{1}$ and incomplete M $\bar{2}$, No. 1968 (Plate 3, fig. 3); C.I.T. Coll. Vert. Pale.

Geological Age and Locality—Middle Pliocene Kern River beds, Kern County, California. C.I.T. Locality No. 49.

SPECIFIC CHARACTERS

Cheek-teeth hypsodont, but crowns show tendency to wear to flat surfaces; without accessory folds although intermediate tubercles may be present or absent. M $\bar{1}$ with divided antero-median cusp; tip of antero-internal re-entrant angle becomes isolated with wear leaving a broad, shallow re-entrant. M $\bar{3}$ relatively unreduced. Pit or foramen in maxillary bone lateral to anterior root of M $\bar{1}$. Size large, slightly exceeding any known fossil species, but approximating that of *Peromyscus nesodytes*.¹

DISCUSSION

Peromyscus pliogenicus is distinguished from all other fossil species of the genus, except *P. antiquus* and *P. nesodytes*, by its large size. Even these two species are somewhat smaller, in length of tooth-row, than the Kern River type.

Compared with *P. antiquus* Kellogg² from the Thousand Creek beds of northern Nevada, *P. pliogenicus* is not only larger but is distinguished by the following selected differences: (1) antero-median cusp of M $\bar{1}$ divided, resulting in an external cusp rather than a narrow sloping ridge as in the Nevadan species; (2) M $\bar{1}$ relatively longer; (3) antero-posterior ridge of M $\bar{2}$ may be slightly less developed; and (4) intermediate tubercles are variably developed, whereas they are entirely absent in *P. antiquus*. Relatively large intermediate tubercles are present in the type of *P. pliogenicus* (Plate 3, figs. 2, 2a), but are absent in the paratype No. 1967. Rudimentary intermediate tubercles are also present in the upper cheek-teeth as demonstrated in the paratype specimen, No. 1968.

Peromyscus nesodytes Wilson,³ from the Santa Rosa Island Pleistocene, approaches *P. pliogenicus* more closely in size than does *P. antiquus*. The Kern River species differs from the island form in the following characters: (1) more hypsodont; (2) internal cusps of cheek-teeth perhaps narrower; (3) intermediate tubercles variably developed, whereas in *P. nesodytes* they appear to be absent. (4) M $\bar{1}$, although of approximately the same antero-posterior diameter, is perhaps less triangular in outline; the tip of the antero-internal re-entrant angle shows a tendency to become isolated, the remainder becoming very shallow and open in contrast to the more permanent V-shaped notch in *P. nesodytes*. In the relatively unworn M $\bar{1}$, the antero-external

¹ It is possible that the character of size is more applicable to the cheek-teeth of *P. pliogenicus* than to the individual as a whole. However, the present fragmentary material does not suggest necessarily that this individual possessed relatively large cheek-teeth.

² L. Kellogg, *op. cit.*, 432–433, fig. 16, 1910.

³ R. W. Wilson, *Jour. Mamm.*, vol. 17, 408–410, 1 fig., 1936.

re-entrant angle is very deep, extending almost to the anterior margin of the tooth. With wear the tip of this re-entrant also becomes isolated. In *P. nesodytes* this re-entrant angle apparently never was so deep, although wear may have obliterated any enamel islet resulting from isolation. (5) Judging from the alveolus, M $\overline{3}$ is less reduced.

Comparative measurements (in millimeters)

	<i>Peromyscus pliocenicus</i>		<i>P. antiquus</i> U.C. No. 12571 (type) Thousand Creek	<i>P. nesodytes</i> C.I.T. No. 1780 (type) Santa Rosa Island Pleistocene
	C.I.T. No. 1966 (type) Kern River beds	C.I.T. No. 1967 (paratype) Kern River beds		
M1-M $\overline{3}$, alveolar length.....		6.1	5.2	5.8
M1-M $\overline{2}$, alveolar length.....		4.3
M1-M $\overline{2}$, occlusal length.....	4.4	4.4	3.9
M1, antero-posterior diameter.....	2.2	2.3	2.0	2.5
M1, transverse diameter.....	1.4	1.5	1.5	1.6
M $\overline{2}$, antero-posterior diameter.....	2.0	2.0	1.8	1.9
M $\overline{2}$, transverse diameter.....	1.6	1.6	1.6	1.6
M $\overline{3}$, antero-posterior diameter.....	1.6	1.5
M $\overline{3}$, transverse diameter.....	1.2	1.3

Peromyscus pliocenicus

C.I.T. No. 1968 (paratype). Kern River beds

M1, antero-posterior diameter.....	2.3
M1, transverse diameter.....	1.5?

Other known fossil forms either are much smaller than *P. pliocenicus* or are closely related to living representatives of the genus.

The Kern River species is clearly separable from Recent species of the genus. It is sharply marked off by its large size from all except members of the subgenera *Megadontomys*, *Peromyscus*, and *Haplomylomys*. Some members of the subgenus *Megadontomys* apparently exceed *P. pliocenicus* in size. However, in the former, supplementary enamel loops and tubercles are highly developed, whereas in our species the accessory tubercles between the primary cusps are apparently not always present, and, most important, no accessory loops or folds of enamel enter into the cheek-tooth pattern of either the superior or the inferior dentition. *Megadontomys* is an inhabitant of southern Mexico and Central America.

Many of the southern species of the subgenus *Peromyscus* are characterized by relatively large size. These species are all smaller than the Californian type and, moreover, possess upper cheek-teeth with supplementary tubercles at the buccal margin which wear to form accessory enamel folds in the cheek-teeth. These supplementary folds may be small but are apparently always present. No. 1968, a maxillary fragment of *P. pliocenicus*,

exhibits rudimentary tubercles. However, these cuspules do not enter into the cheek-tooth pattern.

Members of the subgenus *Haplomylomys* possess cheek-teeth without supplementary tubercles or with such tubercles in a rudimentary state of development. The largest species of the subgenus, *P. californicus*, is distinctly smaller than *P. pliogenicus*. Moreover, the accessory tubercles in the dentition of No. 1966 exceed those of any specimen of *Haplomylomys*.

It is not to be assumed, on the basis of the brief and by no means complete comparisons given above, that *P. pliogenicus* bears a close relationship to any Recent subgenus. As a matter of fact, it is highly improbable that any of the modern subgenera were differentiated as early as the middle Pliocene. Limited comparisons with Recent subgenera are given merely as the simplest means of eliminating from consideration the large number of Recent species. However, it is worth noting that large species were common in the middle Pliocene of the United States, whereas now, except for *P. californicus*, the large peromyscine forms are all southern in distribution. This fact may indicate a general southward movement of many of the Pliocene forms with, of course, considerable evolutionary change with the passing of geologic time.

LAGOMORPHA

Leporidae

Hypolagus near *limnetus* Gazin

Leporid remains are rather abundant in the Kern River collection. These remains include fragmentary rami and maxillæ as well as isolated teeth and skeletal parts. Two species appear to be present, the larger of which is near *Hypolagus limnetus* of the Hagerman fauna.¹ The more complete material representing this form includes No. 1969 (Plate 3, fig. 5), a specimen with the palatal portion of the maxillæ preserved with P3-M2 present on both sides; a left maxillary with P2-M2, No. 1970 (Plate 3, fig. 6); a right ramus with P3-M3, No. 1972 (Plate 2, fig. 5); a left ramus with P3-M2, No. 1973 (Plate 2, fig. 4); and a second left ramus with P4-M2, No. 1974. Although the Kern River form is from an older stage, it agrees with *H. limnetus* in approximate size and in the shape of P3, as well as in depth of re-entrant folds in this tooth. P3 is rather broad with the antero-internal border rounded (Plate 2, fig. 4). The antero-external fold is relatively deep, a point of resemblance to the Hagerman type. The character of the plications on the median re-entrant fold of the upper molariform teeth is apparently similar to that in *H. limnetus*. The fold may be slightly less deep and complex on the average, but there seems to be variation in this regard in the Kern River form.

Hypolagus furlongi Gazin² from Grand View is closely related to *H. limnetus*. However, the Kern River form is apparently distinguished by a less triangular P3 with deeper antero-external fold. Moreover, in P2 of *H. furlongi* the antero-internal fold is deep and crenulated. P2 in the Californian material is more like that of *H. limnetus* and is not crenulated.

Other species of *Hypolagus* do not appear to be closely related to the Kern River type. *H. vetus*, although from an approximately equivalent

¹ C. L. Gazin, Proc. U. S. Nat. Mus., vol. 83, no. 2976, 114-117, figs. 2-3, 1934.

² *Ibid.*, 118-119, fig. 4, 1934.

horizon, is larger and possesses a $P\bar{3}$ in which the antero-external fold is shallower and the outline of the tooth somewhat narrower anteriorly.

Hypolagus edensis Frick¹ from the middle (?) Pliocene Eden beds is smaller than *H. near limnetus*; the inner borders of the lower molariform teeth are rounded, not angulate as in the Kern River form; and the antero-external fold in $P\bar{3}$ is more anterior in position.

Hypolagus? apachensis Gazin² compared with *H. near limnetus* is from an older stage. It is a smaller form with the median fold of the upper molariform teeth less complexly plicated. In addition, $P\bar{3}$ is relatively longer and the antero-external fold in that tooth is shallow.

Lastly, *H. browni* (Hay)³ appears to be more advanced in character of the postero-external fold of $P\bar{3}$ than is the Kern River species. However, the antero-external fold is relatively less deep than in *H. near limnetus*. This species is smaller and from a distinctly later stage (early Pleistocene?).

The Kern River material agrees more nearly with *H. limnetus* from Hagerman than with any other species of the genus. However, it comes from an earlier stage and may represent a distinct species. Since seven or eight species of *Hypolagus*, representing a wide variety of types, are already known, nothing is gained by separating the Kern River species as a distinct type.

Measurements (in millimeters) of Hypolagus near limnetus Gazin

	No. 1971	No. 1970	No. 1969
P2-M3, alveolar length.....	13.1
P2-M2, occlusal length.....	9.3+
P2-M2, alveolar length.....	11.9
P3-M2, occlusal length.....	8.7—	8.4
Greatest width across antero-ventral prominence of zygomatic arches	30.5
Least antero-posterior length of bony palate.....	5.5

	No. 1972	No. 1973	No. 1974
P3-M3, alveolar length.....	13.5	14.1 (a)
P3-M2, occlusal length.....	10.8—
Depth of ramus beneath M1, measured on outside.....	10.6	10.4

(a) Approximate.

¹ C. Frick, Univ. Calif. Pub., Bull. Dept. Geol., vol. 12, no. 5, 348, figs. 52-53, 1921.

² C. L. Gazin, Carnegie Inst. Wash. Pub. No. 404, 67-69, pl. 3, figs. 1-4, 1930.

³ O. P. Hay, Proc. U. S. Nat. Mus., vol. 59, no. 2391, 630-631, 1921; L. R. Dice, Papers Mich. Acad. Sci., Arts, and Letters, vol. 16, 379-382, figs. 8-11, 1932.

Hypolagus small sp.

Several of the *Hypolagus* specimens from the Kern River beds appear to represent a second, smaller species of the genus. The species is represented by No. 1975, a fragment of left ramus with P $\overline{3}$ -M $\overline{1}$, and several isolated teeth. In contrast to the larger Kern River species, P $\overline{3}$ in this type is somewhat elongate and triangular. Only three third lower premolars in the collection appear referable to the species of *Hypolagus* under discussion. All these teeth are somewhat different, including one, No. 1976, with a postero-internal groove on the side of the tooth in evidence as a slight fold on the occlusal surface of the tooth. The antero-external fold in P $\overline{3}$ is fairly deep but shows a tendency to be quite wide. In one specimen, No. 1975, the anterior limb of the fold is parallel to the axis of the tooth. The lower molariform teeth, as compared with those of *H. near limnetus*, may be relatively a little longer antero-posteriorly, but the limited remains available make this character doubtful. The upper molariform teeth, represented by isolated teeth, may possess median re-entrant folds which are less complexly plicated than in the larger species. This statement is also doubtful in view of uncertainty as to the position of the teeth in the maxillary, and since individual variation is seen in this character when large series of teeth are available for comparison. Moreover, if these teeth are viewed from below they appear to be more complexly folded.

Remains of this species are not complete enough to warrant a specific designation. As a matter of fact, the specimens may represent young individuals, and difference in tooth-pattern between this form and *H. near limnetus* from the same locality may be due to age. Comparisons with known small species of *Hypolagus* were made, but because of the limited material available, proved inadequate to reveal any real relationships.

Measurements (in millimeters) of Hypolagus small sp.

	No. 1975
P $\overline{3}$ -P $\overline{4}$, antero-posterior length.....	5.2

PLATE 1

Mylogaulus? cf. *monodon* Cope

FIGS. 1, 4, 5—Isolated right P4's; Nos. 1955, 1952 (reversed), and 1953; $\times 2\frac{1}{4}$.

FIG. 2—Isolated left P4 (reversed); No. 1954; $\times 2\frac{1}{4}$.

FIG. 3—Isolated left P4 (reversed); No. 1956; $\times 2\frac{1}{4}$.

FIG. 6—Isolated right P4; No. 1958; $\times 2\frac{1}{4}$.

FIG. 7—Isolated P4; No. 1957; $\times 2\frac{1}{4}$.

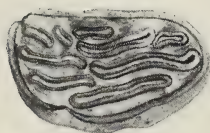
FIGS. 8, 8a, 8b—Left ramus with P4-M3 inclusive; No. 72. Fig. 8, occlusal view, $\times 2\frac{1}{4}$; fig. 8a, intero-lateral view, $\times \frac{3}{4}$; fig. 8b, extero-lateral view, $\times \frac{3}{4}$.

Castor? sp.

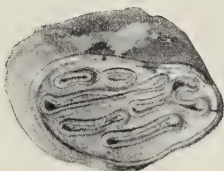
FIGS. 9, 9a—Isolated left M2?; No. 1961; $\times 2\frac{1}{4}$. Fig. 9, occlusal view (reversed); fig. 9a, intero-lateral view.

Sizes of all figures approximate.

Calif. Inst. Tech. Coll. Vert. Pale. Middle Pliocene, Rome, Oregon.



1



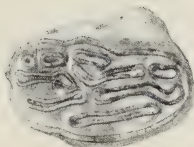
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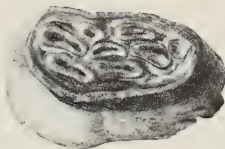
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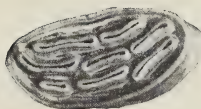
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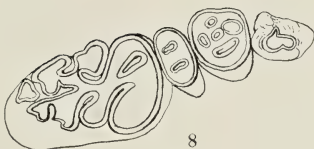
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6



7



8



9



8^a



8^b



9^a

PLATE 2

Hypolagus sp.

FIGS. 1, 1a—Incomplete left ramus with P4-M3; No. 1964. Fig. 1, occlusal view, $\times 2\frac{1}{4}$; fig. 1a, lateral view, $\times 1\frac{1}{2}$. Middle Pliocene, Rome, Oregon.

Goniodontomys disjunctus n. gen. and sp.

FIGS. 2, 2a, 2b—Fragmentary left ramus with M1-M2, genotype specimen; No. 1959. Fig. 2, occlusal view, $\times 9$; fig. 2a, intero-lateral view, $\times 4\frac{1}{2}$; fig. 2b, extero-lateral view, $\times 4\frac{1}{2}$. Middle Pliocene, Rome, Oregon.

Hypolagus vetus (Kellogg)

FIGS. 3, 3a—Incomplete left ramus with P3-M1; No. 1962. Fig. 3, occlusal view, $\times 2\frac{1}{4}$; fig. 3a, lateral view, $\times 1\frac{1}{2}$. Middle Pliocene, Rome, Oregon.

Hypolagus near *limnetus* Gazin

FIG. 4—Incomplete left ramus with P3-M2; No. 1973; $\times 2\frac{1}{4}$; occlusal view. Middle Pliocene, Kern River Beds, California.

FIG. 5—Right ramus with P3-M3; No. 1972; $\times 1\frac{1}{2}$; lateral view. Middle Pliocene, Kern River Beds, California.

Sizes of all figures approximate.

Calif. Inst. Tech. Coll. Vert. Pale.



PLATE 3

Citellus? sp.

FIGS. 1, 1a—Right ramus with $P\bar{4}$ – $M\bar{2}$; No. 1965; $\times 3$. Fig. 1, occlusal view; fig. 1a, lateral view.

Peromyscus pliocenicus n. sp.

FIGS. 2, 2a—Incomplete right ramus with $M\bar{1}$ – $M\bar{2}$, type specimen; No. 1966. Fig. 2, occlusal view (reversed), $\times 6\frac{3}{4}$; fig. 2a, lateral view, $\times 4\frac{1}{2}$.

FIG. 3—Fragment of right maxillary with $M\bar{1}$ and incomplete $M\bar{2}$ (reversed), paratype specimen; No. 1968; $\times 6\frac{3}{4}$.

FIG. 4—Left ramus with $M\bar{1}$ – $M\bar{2}$ (reversed), paratype specimen; No. 1967; $\times 6\frac{3}{4}$.

Hypolagus near *limnetus* Gazin

FIG. 5—Incomplete maxillæ with right $P\bar{3}$ – $M\bar{2}$ and left $P\bar{3}$ – $M\bar{2}$; No. 1969; $\times 1\frac{1}{2}$.

FIG. 6—Fragmentary left maxillary with $P\bar{2}$ – $M\bar{2}$; No. 1970; $\times 2\frac{1}{4}$.

Sizes of all figures approximate.

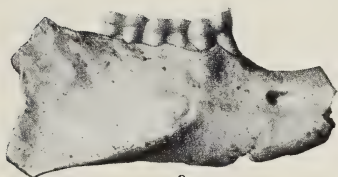
Calif. Inst. Tech. Coll. Vert. Pale. Middle Pliocene, Kern River Beds, California.



1



2



1^a



2^a



3



4



5



6

CONTRIBUTIONS TO PALÆONTOLOGY

II

PLIOCENE RODENTS OF WESTERN NORTH AMERICA

By ROBERT W. WILSON

With two text-figures

[Issued July 23, 1937]

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PLIOCENE RODENTS OF WESTERN NORTH AMERICA

INTRODUCTION

Knowledge concerning the extinct mammal faunas of North America has increased enormously since the beginning of the present century. Certain groups of mammals are known in great detail and fairly satisfactory "trees" showing their phylogenetic relationships have been erected. Other groups are not so well known, but the general course of their history has been traced and little remains but to fill in the gaps and to make minor corrections. On the other hand, a few groups have proved more or less refractory, and the order Rodentia may be regarded as one of the more important of these. Not only are the broader phases of rodent evolution, such as the differentiation of modern families from ancestral stocks, not at all well known, but it is commonly assumed that rodent types are remarkably stable, the same genus, and even species, having an extremely long range in geologic time as compared with those grouped under other orders. Hence the rodents at present are regarded by many as an order offering but little from an evolutionary standpoint, and as barred by their stability from any use in detailed stratigraphy and correlation.

The views expressed above are those held by most palæontologists. They are, however, views inherited for the most part from older workers, handicapped by lack of sufficient material and knowledge of the stratigraphic location of that material. Most present-day workers on fossil rodents, although not agreeing among themselves as to the limiting possibilities of rodent research, feel that the older views are not altogether correct.

Before proceeding to a discussion of the scope of the present paper, it seems pertinent to outline briefly the various lines of rodent research and the advances made thus far, as well as to indicate the results which may be expected from a study of fossil rodents.

Some of the more fundamental types of research relate to the differentiation of modern families from a common rodent stock. At present, extremely little is known and widely divergent views are held with regard to the time and manner of that differentiation. If results are to be obtained in this direction, it will be particularly through a careful study of middle and upper Eocene rodents. A study of all material now available probably would extend our knowledge demonstrating the Eocene ancestry of the modern families. It is likely, however, that final proof will have to await the discovery of more perfect specimens and the acquisition of more extensive upper Eocene rodent

faunas. One of the chief drawbacks to any work on the differentiation of modern families lies in the absence of skull material from critical horizons. This view appears more likely to account for the lack of intermediate types than the alternative one, presented by Miller and Gidley (1918), that the Rodentia were already differentiated at the time of their first appearance in the palæontological record.

A second direction of research is the establishment of phylogenetic lines within the family. Fossil materials known at the present time are hardly sufficient for detailed phylogenetic studies. They suffice in most cases to establish the broad lines of evolution, or at least to suggest such lines.

A third field of investigation is concerned primarily with the description of rodent faunas from various stages. This type of research has value in enlarging our picture of the past mammalian life, and in furnishing a basis for study in the previously mentioned fields. At present even this work is neglected, and large collections of undescribed rodents are in existence. Omission of studies of this kind has proved a stumbling block for more ambitious projects along other lines. Of course in connection with such investigations phylogenetic studies should not be neglected.

An outgrowth of faunal studies is the recognition of the time range of various genera and species, and the establishment of important index fossils. With increasing knowledge of fossil rodents it has become apparent that certain groups, at least, will ultimately furnish distinctive horizon markers. At present the number of such index fossils is few. However, if the existing rodents, which embrace more different types than all other mammals combined, have descended as commonly believed from a single lower Eocene genus or at most from several closely related genera, it is obvious that the Tertiary radiation is very great, and consequently the group should furnish many such markers.

The nature of the present paper practically limits the fields of discussion to the last two mentioned above. All present-day families were established long before the opening of Pliocene time. The short duration of that epoch, as well as the fragmentary nature of the material, sharply limit the observable evolution of the order during that time. Pliocene rodent assemblages are not very abundant nor are they complete, but this is likewise true of other mammalian remains from the epoch, so that any data which may be obtained as to the stratigraphic position of faunas are relatively more important than similar data for other divisions of the Tertiary.

The term Pliocene is here used to include not only all true Pliocene occurrences but also the doubtful Miocene-Pliocene and Pliocene-Pleistocene faunas. In a general way this covers a period embraced

by the European time sequence, Pontian to Sicilian. The present paper deals only with Pliocene faunas from western North America, but since no Pliocene rodent types have been recorded elsewhere in North America, the study is not actually limited geographically.

This review is the result of studies that have been made on Pliocene rodent faunas from: (1) Kern River beds of California; (2) Smiths Valley, Nevada; (3) Rome, Oregon; (4) Coso Mountains, California; (5) Hagerman, Idaho; and (6) Grand View, Idaho. During the course of the work, examination was also made in whole or in part of faunas from the following localities: (1) Bartlett Mountain, Oregon; (2) Fish Lake Valley, Nevada (Esmeralda fauna of Stirton); (3) Rattlesnake, Oregon; (4) Thousand Creek, Nevada; and (5) San Pedro Valley, Arizona (Curtis fauna). Other Pliocene rodent collections are known to the author only through published descriptions. Detailed accounts of faunas in the California Institute of Technology collections have already been published (Wilson, 1932, 1933, 1934, 1935, 1936, and 1937).

While lack of familiarity with certain faunas, especially those of the Great Plains Pliocene, has served to restrict observations on several phases of the work, it is hoped that the succeeding pages will help to bring together widely separated data on Pliocene Rodentia. The treatment is faunal rather than taxonomic, and, moreover, represents only a progress report, inasmuch as any final statement must rest on the acquisition of more extensive collections.

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I wish gratefully to re-acknowledge the loan of fossil material from the Museum of Paleontology, University of California, and the United States National Museum. The latter institution has also assisted the study by the loan of Recent comparative material. Similar material has been kindly made available from the Donald R. Dickey Collection of Recent mammals at the California Institute.

Information for this paper has been furnished by a number of individuals and drawn from many published sources, partial acknowledgment of which is made in the citations and in the appended bibliography.

PREVIOUS STUDIES OF NORTH AMERICAN FOSSIL RODENTS

Early workers in the field of North American fossil rodents were first Joseph Leidy, followed by E. D. Cope, O. C. Marsh, and finally W. D. Matthew. Other palæontologists contributed, to be sure, but by far the bulk of the work was carried on by these four men. Their investigations covered a period extending from the first studies of Leidy down to 1910. It was mainly a period of description with little or no attempt to outline phylogenetic trends. It is true that relationships of various extinct types of rodents to modern forms were recognized, sometimes with surprising accuracy considering the poor material available for study. On the other hand, we find identifications of John Day lagomorphs as *Lepus*, lower Oligocene ischyromyids as *Sciurus*, and John Day castorids as *Castor*. Perhaps it was such identifications that established the belief that rodents were extremely stable forms.

It is difficult to evaluate the importance of the work by Leidy, Cope, and Marsh, and the earlier studies of Matthew. Leidy, publishing chiefly in the proceedings of the Academy of Natural Sciences of Philadelphia and in various government reports, commands attention principally because his work was the starting point for later, more comprehensive studies. Cope was probably the dominant figure of the first period of rodent research in this country. His researches are summarized in "The Vertebrata of the Tertiary Formations of the West" (1884). Marsh's contribution is relatively unimportant as compared with that of the other three palæontologists. His most important work was in connection with the building of a large collection of Bridger rodents which apparently has never been completely described or even prepared for study. With Cope's death, Matthew became the leading worker in the field. Practically all his contributions are to be found in the various publications of the American Museum.

The modern period of fossil rodent research may be dated from the publication by Matthew, in 1910, of his classic contribution "On the Osteology and Relationships of *Paramys*, and the Affinities of the Ischyromyidæ." The view expressed in this paper that the order of rodents is descended from a *Paramys* or *Paramys*-like ancestor of the lower Eocene is accepted at present by most workers in the field of rodent palæontology. The only exception taken to this concept by American workers was made in 1918 by Miller and Gidley in their "Synopsis of the Supergeneric Groups of Rodents." This paper was originally intended as a preliminary report on an ambitious program of study of the entire field of fossil and living rodents. The final report has never been published. The synopsis presented many new ideas, extremely discouraging to further rodent work if they could be

proved. As has been pointed out at various times by several palæontologists, this paper is more an artificial key for the recognition of supergeneric or family groups than a genetic classification. The principal view presented by Miller and Gidley, as mentioned previously, is that all rodent families were completely differentiated at the time of their first appearance in the palæontological record.

A more recent phase of the modern period has been research on family or subfamily groups of rodents. Here might be mentioned one European work: Schaub's "Die hamsterartigen Nagetiere des Tertiärs" (1925), which is perhaps the first accurately written and accurately illustrated publication dealing with the evolution of a phylum of rodents. Recent American publications of this type have been: "Evolution and Relationship of the Heteromyid Rodents," by A. E. Wood (1935), and "A Review of the Tertiary Beavers," by R. A. Stirton (1935).

A review of the literature dealing exclusively with Pliocene rodents is difficult to present. Most of the work accomplished to date has been in connection with descriptions of other mammals. Papers dealing exclusively with Pliocene rodents are limited in number. In 1910, Miss Louise Kellogg published a description of a "Rodent Fauna of the Late Tertiary Beds at Virgin Valley and Thousand Creek, Nevada." J. W. Gidley's "Preliminary Report on Fossil Vertebrates of the San Pedro Valley, Arizona, with Descriptions of New Species of Rodentia and Lagomorpha" appeared in 1922. More recently, in 1930, E. Raymond Hall issued a report on the "Rodents and Lagomorphs from the Later Tertiary of Fish Lake Valley, Nevada." Lastly, several papers by the present author concerning Pliocene rodents have been presented from time to time since 1932. The bibliography lists these publications (1932, 1933, 1934, 1935, 1936, and 1937).

THE NATURE OF NORTH AMERICAN TERTIARY RODENT FAUNAS

TAXONOMIC CLASSIFICATION

The taxonomic classification of rodents used in this paper is in no sense original. Perhaps it is closest to Simpson's arrangement presented in 1931. Certain changes have been made where such changes appear desirable to the author or where a compromise with several systems seems advantageous. The present arrangement has the advantage or disadvantage, depending on the point of view, of being very conservative. The following outline omits families not recorded from North America, as well as the families Dipodidæ and Muridæ, which have been doubtfully recorded. It is intended principally as a

guide to later discussions concerning particular families and their representatives.

Order Rodentia (rodents in a strict sense)

Suborder Sciuromorpha (squirrel-like rodents)

Superfamily Aplodontoidea

*† Family Ischyromyidæ

† Family Mylagaulidæ

Family Aplodontiidæ (mountain-beavers or sewellels)

Superfamily Sciuroidea

Family Sciuridæ (squirrels)

Superfamily Castoroidea

Family Castoridæ (beavers)

Superfamily Geomyoidea

Family Heteromyidæ (pocket-mice and kangaroo-rats)

Family Geomyidæ (pocket-gophers)

Suborder Myomorpha (mouse-like rodents)

Superfamily Myoidea

Family Cricetidæ (rats and mice)

Superfamily Dipodoidea

Family Zapodidæ (jumping-mice)

Suborder Hystricomorpha (porcupine-like rodents)

Superfamily Hystricoidea

Family Erethizontidæ (New World porcupines)

* Family Caviidæ (guinea-pigs)

Order Lagomorpha (rabbits, hares, and pikas)

Family Ochotonidæ (pikas)

Family Leporidæ (rabbits and hares)

* Not present in Pliocene.

† Extinct.

The popular term rodent embraces two orders of mammals which may have only a very distant relationship. One order, the Lagomorpha, which includes the hares, rabbits, and pikas, is a rather restricted group and has remained remarkably stable from its first appearance in the fossil record. The second order, that of the Rodentia, or true rodents, is marked by an extreme diversity of type originating from a central stock. These forms consequently exhibit parallelism among themselves to an extraordinary degree. The present study will include both orders, since the Lagomorpha are so limited as to make separate treatment not very desirable.

The classification of the Rodentia used here is the old threefold division, namely, the Sciuromorpha or squirrel-like rodents, the Myomorpha or mouse-like rodents, and the Hystricomorpha or porcupine-like rodents, based principally on the character of the masseter muscle and its attachment to the skull. This division is not universally accepted or entirely satisfactory, but in the case of North American rodents it is a fairly logical one and very convenient. The North American sciuromorphs include the mountain-beavers,

squirrels, beavers, gophers, pocket-mice, and kangaroo-rats among living forms, and the ischyromyids and mylagaulids among extinct types. These forms are characterized by relatively small infraorbital foramina in which no invasion by the masseter muscle takes place. Moreover, the angle of the ramus appears to originate on the inferior border of the ramus, and not upon the side as in the Hystricomorpha.

Only two families of North American myomorphs have been definitely recorded, namely the Cricetidae, including indigenous rats and mice, and the Zapodidae or jumping-mice. In these forms the infraorbital foramen becomes enlarged and is traversed by a branch of the masseter muscle. The angle of the ramus is similar to that of the Sciuiomorpha.

The North American Hystricomorpha include representatives of the Erethizontidae or porcupines, and the Caviidae or guinea-pigs. In these forms the infraorbital foramen is extremely large and transmits the masseter medialis. The angle of the ramus appears to originate on the side of the ramus, in contrast with the more normal angle of the Sciuiomorpha and Myomorpha. This group is relatively unimportant among North American rodents. Our only known forms are invaders from South America.

SCIUIOMORPH PREDOMINANCE IN NORTH AMERICA

The Sciuiomorpha is the most primitive of the suborders, and probably gave rise to the other two. In North America it is the dominant group of the Tertiary. All sciuiomorph families are represented excepting the anomaluroids. The mylagaulids, gophers, and heteromyids are confined to North America, and the aplodontids are represented elsewhere only by a single Pliocene specimen from Asia.

In the ascendancy of the sciuiomorphs, North America stands in contrast to most other continents, in which, during the Miocene and Pliocene at least, the higher types of Rodentia are the dominant types. In Asia most of the later Tertiary forms are myomorphs; in South America the fauna is almost exclusively hystricomorph. For these reasons study of North American rodents is limited essentially to the Sciuiomorpha. Studies concerning the evolution of the Aplodontiidae, Mylagaulidae, Geomyidae, and Heteromyidae should furnish, and are furnishing, important data on the evolution of these families, since the groups mentioned are virtually confined to this continent. North American fossil Myomorpha may yield a limited amount of data on certain members of the Cricetidae and Zapodidae, but the seat of higher rodent evolution is elsewhere. The date of appearance of certain hystricomorph types may eventually afford horizon markers, but the evolution of this group occurred farther to the south.

PLIOCENE RODENT FAUNAS

The relative position of most of our Pliocene faunas is more or less agreed upon. However, there is wide divergence of view as to where the Miocene-Pliocene and Pliocene-Pleistocene boundary lines should be drawn. Consequently, unless one makes clear what is meant by lower Pliocene, for example, considerable confusion may arise. The lower Pliocene of one author may include the Thousand Creek, of another the Fish Lake Valley beds. To say that the extinct beaver *Eucastor* is characteristic of the lower Pliocene is ambiguous if the statement is not accompanied by a qualifying explanation, since the characteristic Thousand Creek beaver is *Dipoides*.

In the present paper a threefold division of the Pliocene into lower, middle, and upper is adopted. The lower division includes such faunas as the Fish Lake Valley or Esmeralda, which would be considered upper Miocene or perhaps transitional by some authorities. It is roughly equivalent to the so-called Pontian faunas of Europe and Asia. The author expresses no particular convictions in placing the faunas assigned to this division in the lower Pliocene instead of the upper Miocene, but it seems a rather convenient arrangement. As a matter of fact, if the extreme views of some authors were applied to the lower and upper boundaries of the Pliocene, this period would be reduced almost to the vanishing point. In any case, the placing of boundary lines is frequently an academic question not always consistent with the facts of Nature.

The middle Pliocene of this paper includes such faunas as the Thousand Creek, Rattlesnake, and upper Snake Creek. The Pliocene age of these faunas is agreed upon by all American palæontologists. They are roughly comparable to the Plaisancian faunas of Europe.

The division termed upper Pliocene includes faunas from Grand View, Hagerman, the upper Etchegoin, and San Pedro Valley. These faunas correspond in part to the lower Pleistocene of some authors. Their European equivalents are the Norwich Crag and Val d'Arno. There seems some justification for the belief that at least part of the present author's upper Pliocene should be termed lower Pleistocene. This question will be discussed in some detail in a later and more convenient place.

The following rodent faunal lists are as complete and accurate as it is possible to make them. Determinations have been brought up to date whenever feasible, and some genera of doubtful presence eliminated. It is extremely difficult to give accurate lists for the Great Plains Pliocene faunas, since considerable reworking of materials and indistinct contacts seem to be characteristic of these deposits. Moreover, the exact locality of many types is not known, since the collecting of these specimens occurred in the days when ac-

curate location of materials was not made. Rodent faunas that are too poorly known and possess no particular importance are omitted.

LOWER PLIOCENE

FISH LAKE VALLEY FAUNA (ESMERALDA OF STIRTON)

Locality—Fish Lake Valley, Esmeralda County, Nevada.

Rodentia

Family Mylagaulidæ

Mylagaulus sp. (cf. *monodon* Cope)

Family Castoridæ

Eucastor dividerus Stirton

Family Heteromyidæ

Perognathoides tertius (Hall)

Perognathoides quartus (Hall)

Family Cricetidæ

Peromyscus dentalis Hall

Macrognathomys nanus Hall

Lagomorpha

Family Leporidæ

Hypolagus cf. *vetus* (Kellogg)

Sylvilagus? sp.

In the original description of the fauna, E. Raymond Hall (1930) figured an isolated tooth which he doubtfully referred to the Geomyidæ. Hall tentatively identified the specimen as *Entoptychus?* sp. Recently, A. E. Wood (1936a) has suggested that the fragment is probably a deciduous upper premolar of a lagomorph.

SIESTA FORMATION

Locality—Berkeley Hills, California.

Rodentia

Family Castoridæ

Eucastor lecontei (Merriam)

Lagomorpha

Family Leporidæ

Lepus sp.

The reference of lagomorph material to *Lepus* by J. C. Merriam is probably incorrect. Since there is no published description of the material, the original designation is retained, but the form represented is probably *Hypolagus* or some similar type.

VALENTINE BEDS

Locality—Valentine, Nebraska.

The Valentine beds are usually designated as upper Miocene, lower Pliocene, or transitional. Recent work has indicated that more than

one faunal horizon is present, and the older faunal lists are presumably of composite nature. Johnson (1936) and Stirton and McGrew (1935) agree that at least two faunas can be distinguished. The older is apparently of upper Miocene or transitional age, and antedates any other fauna listed as lower Pliocene in this paper. The name Valentine fauna has been applied to this assemblage by Johnson, and Niobrara River by Stirton and McGrew. Since the present author is in no position to judge the merits of either name, and since Valentine has been adopted by most palæontologists including those of the Nebraska Geological Survey and the Nebraska State Museum, this term will be used in the present paper. The younger fauna has been designated the Burge fauna by Stirton and McGrew, and the name was subsequently adopted by Johnson. The latter author has termed the beds carrying the Burge fauna, the Burge sands. According to Stirton and McGrew (1935, p. 129), the Burge fauna appears to be equivalent to the Fish Lake Valley assemblage.

Until the Valentine and Burge faunas are revised and restudied in detail in the light of more recent knowledge, rodent faunal lists of these assemblages are to be regarded as tentative. The Valentine rodent fauna presented below is probably in part composite, but is listed for completeness. Starred (*) forms are presumably from the "type" quarries of the Valentine.

Valentine Fauna

Rodentia

Family Mylagaulidæ

Mylagaulus "monodon" Cope

Family Castoridæ

* *Monosaulax pansus* (Cope)

* *Monosaulax curtus* (Matthew and Cook)

* *Monosaulax* or *Eucastor* sp.

Eucastor cf. *tortus* Leidy

Family Heteromyidæ

* *Cupidinimus nebraskensis* Wood

* ?*Diprionomys* sp. nov. indet. (determination by Wood)

* Heteromyid sp. (an undescribed form related to *Microdipodops*, U. C. Coll.)

Diprionomys agrarius Wood (Devil's Gulch beds, *Teleoceras* level)

Family Geomyidæ

?*Geomys bisulcatus* Marsh (listed by Cook and Cook, 1933)

Lagomorpha

Some remains recorded

Burge Fauna

Rodentia

Mylagaulidæ

Mylagaulus sp.

Castoridæ

Eucastor sp.

MIDDLE PLIOCENE

BARTLETT MOUNTAIN FAUNA

Locality—Bartlett Mountain, near Drewsey, Harney County, Oregon.

Rodentia

Family Mylagaulidæ

Mylagaulus cf. *monodon* Cope

Family Sciuridæ

Citellid sp.

Family Castoridæ

Dipoides? sp.

Family Geomyidæ

Geomyid? sp.

Lagomorpha

Family Leporidæ

Leporid sp.

The Bartlett Mountain fauna is an undescribed assemblage in the collections of the California Institute of Technology. It was discovered by Chester Stock and E. L. Furlong in 1928.

RATTLESNAKE FORMATION

Locality—Dayville, Grant County, Oregon.

Rodentia

Family Sciuridæ

Otospermophilus gidleyi Merriam, Stock, and Moody

Family Castoridæ

Dipoides sp.

Lagomorpha

Family Leporidæ

Hypolagus near *vetus* (Kellogg)

W. D. Matthew (1933) has objected strenuously to referring the Rattlesnake citellid to the Recent subgenus *Otospermophilus*. Most of his very cogent remarks were based on characters exhibited in *Sciurus angusticeps*, a middle Miocene or lower upper Miocene specimen from the Deep River beds. It is possible, however, that in view of the considerably later age of *Otospermophilus gidleyi*, the genus *Citellus* was sufficiently differentiated to have distinct representatives of its subgenera in existence. I am inclined to agree with the view expressed by Matthew, since none of the middle Pliocene representatives of *Citellus* which I have seen appears to have progressed beyond a *Callospermophilus* or *Otospermophilus*-like stage in the dentition. As a matter of fact, Dr. Gidley, when describing the specimen for Merriam, Stock, and Moody, regarded its reference to *Otospermophilus* as tentative.

KERN RIVER DEPOSITS

Locality—Bakersfield Quad., U. S. Geol. Surv., N.E. $\frac{1}{4}$ Sec. 26, T. 28 S., R. 28 E., Mt. Diablo Base and Mer., Kern County, California.

Rodentia

Family Sciuridæ

Citellus? sp.

Family Cricetidæ

Peromyscus pliogenicus Wilson

Lagomorpha

Family Leporidæ

Hypolagus near *limnetus* Gazin

Hypolagus small sp.

This fauna has been described in a recent publication entitled "New Middle Pliocene Rodent and Lagomorph Faunas from Oregon and California" (Wilson, 1937).

SMITHS VALLEY FAUNA

Locality—Smiths Valley, Lyon County, Nevada.

Rodentia

Family Aplodontiidae

Aplodontid sp.

Family Sciuridæ

Citellus? sp.

Family Geomyidæ

Pliosaccomys dubius Wilson

Family Cricetidæ

Peromyscus near *antiquus* Kellogg

Family Zapodidae

Pliozapus solus Wilson

Lagomorpha

Family Leporidæ

Leporid sp.

The Smiths Valley rodent assemblage has been described recently by the author (1936).

THOUSAND CREEK BEDS

Locality—Thousand Creek, Humboldt County, Nevada.

Rodentia

Family Mylagaulidæ

Mylagaulus cf. *monodon* Cope

Family Aplodontiidae

Liodontia furlongi Gazin

Family Sciuridæ

Marmota nevadensis (Kellogg)

Marmota minor (Kellogg)

Citellus sp.

Family Castoridae

Dipoides sp.

Family Heteromyidae

Diprionomys parvus Kellogg

Cupidinimus magnus (Kellogg)

Family Cricetidae

Peromyscus antiquus Kellogg

Lagomorpha

Family Leporidae

Hypolagus vetus (Kellogg)

Liodontia furlongi was described originally by E. L. Furlong (1910) as *Aplodontia alexandræ*. The latter species included specimens from both Virgin Valley and Thousand Creek. Subsequently, Miller and Gidley (1918, p. 440) made *A. alexandræ* the type of a new genus, *Liodontia*. Finally, C. L. Gazin (1932, pp. 64-65) separated the Thousand Creek specimens of *alexandræ* as a distinct species, *L. furlongi*.

The rodent species described by Miss Kellogg (1910) as *Entoptychus minimus* has been referred to the genus *Diprionomys* by A. E. Wood.¹ Wood considers *D. minimus* as "a previously unknown species of *Diprionomys*." It is possible that *D. minimus* is synonymous with *D. parvus* from the same beds, and that it represents a relatively unworn dentition of the latter species. P₄ of *D. parvus*, although very close in pattern to the comparable tooth in *D. minimus*, seems much larger. However, difference in stage of wear may account for this difference in size. (1) Jaws are approximately of same size. (2) The teeth of *D. minimus* do not fill their alveoli, an indication that they have not attained their maximum size. Moreover, P₄ appears to widen toward its base. (3) If *Diprionomys* is a heteromyine, it should be noted that in the genus *Liomys* P₄ progressively increases in area of wearing surface as the tooth is worn.

Cupidinimus magnus was described originally as *Diprionomys magnus*. The species was transferred to the present genus by A. E. Wood (1935).

ROME FAUNA

Locality—Rome, Malheur County, Oregon.

Rodentia

Family Mylagaulidae

Mylagaulus? cf. *monodon* Cope

Family Castoridae

Dipoides stirtoni Wilson

Castor? sp.

¹ A. E. Wood, Fossil Heteromyid Rodents in the Collections of the University of California, (abstract) Preliminary List of Titles and Abstracts, 48th Ann. Meeting G. S. A., 1935; Amer. Mus. Nov., No. 866, 24-25, 1936.

- Family Cricetidae
 - Goniodontomys disjunctus* Wilson
- Lagomorpha
 - Family Leporidae
 - Hypolagus vetus* (Kellogg)
 - Hypolagus* sp.

There may be some doubt as to the association of the *Castor?* species with the remaining rodent fauna. The occurrence of the specimen in an area isolated from that in which the other rodents were obtained, and the presence of beds of possible upper Pliocene or Pleistocene age in the vicinity, raise this question. However, the association in the field of *Castor?* with *Pliohippus* teeth and the characters exhibited by the specimen itself obviate this possibility to a large extent.

This fauna has been recently described by the author (1937).

UPPER SNAKE CREEK BEDS

Locality—About twenty miles south of Agate, Sioux County, Nebraska.

Rodentia

- Family Mylagaulidae
 - Mylagaulus monodon* Cope
 - Mylagaulus sesquipedalis* Cope
- Family Sciuridae
 - Sciurus* cf. *aberti* Woodhouse
- Family Castoridae
 - Eucastor* cf. *tortus* Leidy
 - Eucastor* sp.
 - Dipoides* prob. n. sp. (according to Stirton)
 - Castor* cf. *californicus* Kellogg
- Family Heteromyidae
 - Perognathus coquorum* Wood
- Family Geomyidae
 - ? *Thomomys* sp.
 - ? *Geomys* sp.

As in the case of the Valentine, the upper Snake Creek beds of the Great Plains possess apparently a mixed fauna. The rodent assemblage given above seems also to include forms coming from several ages. Noticeably is this so in the presence of both *Eucastor* and *Dipoides*, especially with associated *Castor*. Among the Geomyidae I have listed both *Geomys* and *Thomomys*. Both genera are sometimes given as occurring in the upper Snake Creek beds, but apparently this is an error. Matthew in 1924 (p. 66) lists only *Thomomys*, known by a single ramus without teeth. Matthew in an earlier contribution to the Snake Creek faunas mentioned the presence of *Geomys* as evidenced by a lower jaw without dentition. Probably a

single specimen has accounted for both determinations, and the later assignment is Matthew's final opinion on the specimen.

While the upper Snake Creek rodent assemblage has been given, its apparent composite nature militates against its use in correlation, and the fauna is listed only for the sake of completeness.

EDSON BEDS

Locality—Near Edson, Sherman County, Kansas.

Rodentia

Incertæ sedis

Kansasimys dubius Wood

Family Mylagaulidæ

Mylagaulus monodon Cope

Family Sciuridæ

Sciurus sp.

The genus *Kansasimys* Wood cannot be assigned very well to any known family of rodents. Moreover, as A. E. Wood (1936b) has mentioned, it does not seem advisable to erect a new family for its reception. On the basis of dental characters, this genus might be assigned to the Ischyromyidæ of the present paper, since it possesses characters found in one or another of the varied early Tertiary types which are designated here collectively as the Ischyromyidæ. However, the forward extension of the masseteric fossa in the jaw of *Kansasimys* would prohibit allocation of the genus to this family. Little else than the primitive development of the masseter muscle is shared in common by the genera grouped by W. D. Matthew under the Ischyromyidæ.

UPPER PLIOCENE

UPPER ETCHEGOIN FORMATION (SAN JOAQUIN CLAY)

Locality—Southwestern San Joaquin Valley, California.

Rodentia

Family Castoridæ

Castor californicus Kellogg

Family Cricetidæ

Mimomys primus (Wilson)

Castor californicus is recorded from the Kettleman Hills, and *Mimomys primus* from the Buttonwillow gas field, some distance away. However, the stratigraphy of the west side of the San Joaquin Valley is rather well known and the specimens both come from the San Joaquin clay. According to Barbat and Galloway (1934), *Mimomys* is from a higher zone (zone B) than *Castor* (zone C).

COSO MOUNTAINS FAUNA

Locality—Coso Mountains, Inyo County, California.

Rodentia

Family Cricetidae

Mimomys primus (Wilson)

Lagomorpha

Family Leporidae

Hypolagus near *limnetus* Gazin

Hypolagus small sp.

Contributions to the mammalian fauna of the Coso Mountains have been made by Stock, Wilson, and Schultz. J. R. Schultz is now preparing a complete statement of the fauna and its faunal and age relationships.

HAGERMAN LAKE BEDS

Locality—Hagerman, Twin Falls County, Idaho.

Rodentia

Family Sciuridae

Citellus? sp.

Marmot sp. (Gazin, 1936, p. 285)

Family Castoridae

Castor sp. (On the whole, intermediate between *C. californicus* and *C. canadensis*, according to Stirton, 1935, pp. 446-447)

Family Geomyidae

Thomomys gidleyi Wilson

Family Cricetidae

Mimomys primus (Wilson)

Ondatra idahoensis minor Wilson

Lagomorpha

Family Leporidae

Hypolagus near *vetus* (Kellogg)

Hypolagus limnetus Gazin

Alilepus? *vagus* Gazin

The marmot and beaver material was not examined by the present author.

GRAND VIEW FAUNA, IDAHO FORMATION (?)

Locality—Near Grand View, Owyhee County, Idaho.

Rodentia

Family Castoridae

Castor cf. *accessor* Hay

Family Cricetidae

Synaptomys vetus Wilson

Mimomys? *parvus* Wilson

Ondatra idahoensis idahoensis Wilson

Family Erethizontidae

Erethizon bathygnathum Wilson

Lagomorpha

Family Leporidae

Hypolagus furlongi Gazin

Both the Grand View and Hagerman faunas come from beds which in the past have been called the Idaho formation. C. L. Gazin in various papers on the Hagerman fauna has referred to the beds near Hagerman as the Hagerman lake beds. The two faunas are probably separated somewhat in time, the Hagerman fauna being slightly older.

BENSON FAUNA (SAN PEDRO VALLEY BEDS)

Locality—Near Benson, Cochise County, Arizona.

Rodentia

Family Sciuridae

Citellus bensoni Gidley

Family Heteromyidae

Dipodomys minor Gidley*Cupidinus magnus* (Kellogg)

Family Geomyidae

Geomys minor Gidley*Cratogeomys bensoni* Gidley

Family Cricetidae

Peromyscus brachygnathus Gidley*Peromyscus minimus* Gidley*Eligmodontia arizonæ* Gidley*Onychomys bensoni* Gidley*Sigmodon medius* Gidley*Neotoma fossilis* Gidley

Lagomorpha

Family Leporidae

Lepus, 2 sp.*Sylvilagus* or *Brachylagus* sp.

CURTIS FAUNA (SAN PEDRO VALLEY BEDS)

Locality—Near Benson, Cochise County, Arizona.

Rodentia

Family Sciuridae

Citellus cochisei Gidley

Family Heteromyidae

Perognathus sp.*Dipodomys minor* Gidley*Dipodomys gideyi* Wood

Family Geomyidae

Geomys persimilis Hay

Family Cricetidae

Onychomys pedroensis Gidley*Sigmodon curtisi* Gidley*Sigmodon minor* Gidley*Neofiber?* sp.

Lagomorpha

Family Leporidae

Lepus sp.

Neofiber? species, known from an incomplete upper molar, appears to be generically distinct from *Neofiber* in possessing rooted cheek-teeth. Perhaps the specimen is referable to one of the smaller species of *Ondatra*, such as *O. idahoensis*.

The Curtis and Benson mammalian assemblages, exclusive of the rodents, suggest a difference in age. However, both faunas seem to come from approximately the same stratigraphic horizon, in the same formation. While the rodent faunas do not suggest any great difference in age, few species are found to be common to both.

The problem of the San Pedro Valley faunas is also confused by a somewhat anomalous association of Pliocene and Pleistocene types among the larger mammals. The apparent association of *Lepus* with some of the more primitive types of larger mammals is also confusing. The problem of these faunas will be discussed in more detail elsewhere.

PLIOCENE RODENT EVOLUTION

FAMILY ISCHYROMYIDÆ

The Ischyromyidæ have not been recorded from the Pliocene. Their last appearance may have been in the John Day faunas. *Kansasimys* Wood (1936b), a genus of uncertain affinities, may be related to the ischyromyids, but the probability is not very great. Comments on this rodent type have been made in an earlier section of the present paper. It might be added that A. E. Wood has compared this genus on the one hand with the cylindrodonts and the ischyromyids (s.s.), and on the other with *Sciuravus*.

FAMILY MYLAGAULIDÆ

This family of fossorial rodents seems to become extinct by the end of the middle Pliocene. It has not been certainly recorded from any upper Pliocene beds.

The evolution of the family is not well known. Even the important question of individual and age variation has not been solved. There are probably two distinct phyla, one horned, the other hornless. The alternative view that the presence of horns is a sex character seems less likely; the absence of horns would place the female at a considerable disadvantage, since the horns apparently were used in digging. Moreover, there seems to be a preponderance of hornless types. Of the several skulls in the California Institute collections, none exhibits horns.

Horned mylagaulid types may not occur above the lower Pliocene. Of the two specimens with horns which have been described, *Ceratogaulus* is from the Pawnee Creek beds, and *Epigaulus* from the Republican River. Gidley in his original description of the latter genus

referred the beds from which it came to the upper Miocene. However, the Republican River is usually considered as of lower Pliocene age. Since the beds are generally placed as slightly younger than the

Order or Suborder	Family	Genus	Lower Pliocene	Middle Pliocene	Upper Pliocene
	Incertæ sedis	*Kansasimys			
Sciuromorpha	Mylagaulidæ	*Mylagaulus *Epigaulus		? ? ?	
	Aplodontiidæ	*Liodontia			
	Sciuridæ	Sciurus			
		Citellus			
		Otospermophilus		? ? ?	? ? ?
		Marmota			
	Castoridæ	*Monosaulax	? ? ?	? ? ?	
		*Eucastor			
		*Dipoides			
		Castor			
	Heteromyidæ	Perognathus			
		*Perognathoides			
		Dipodomys			
		*Cupidinimus			? ? ?
		*Diprionomys			
	Geomyidæ	*Pliosaccomys			
		Thomomys	? ? ?		
		Geomys	? ? ?	? ? ?	
		Cratogeomys			
Myomorpha	Cricetidæ	Peromyscus			
		Eligmodontia			
		*Macragnathomys			
		Onychomys			
		Sigmodon			
		Neotoma			
		*Goniodontomys			
		Synaptomys			
		*Mimomys			
		Ondatra			
		Neofiber			? ? ?
	Zapodidæ	*Pliozapus			
Hystricomorpha	Erethizontidæ	Erethizon			
Lagomorpha	Leporidæ	Lepus	? ? ?		? ? ?
		Sylvilagus			
		*Hypolagus			
		*Alilepus (?)			

FIG. 1—Distribution of Pliocene rodent and lagomorph genera

- Present.
 - - - - - Undoubtedly present but not recorded (present both before and after a particular stage).
 ? ? ? Questionably present for one or more of the following reasons: (1) taxonomic position doubtful; (2) stratigraphic position doubtful; (3) age of beds doubtful.
 * Extinct.

Valentine, their age is practically equivalent to that of some of the formations referred to the middle Pliocene in this paper. Moreover,

it has been suggested that the Republican River is in part composite (see Simpson, 1933, p. 107) and that the *Epigaulus* locality (Long Island quarry) is of later age than that usually assigned to the formation, and hence typically middle Pliocene (Teilhard and Stirton, 1934, p. 284, table 3).

Two species of mylagaulids have been definitely recognized in the Pliocene, namely, *Mylagaulus monodon* and *M. sesquipedalis*. The types of both species are, however, from beds of questionable age. The two are distinguished by the fact that *M. sesquipedalis* is smaller, possesses fewer lakes, the lakes are less elongate, and more irregularly arranged. *M. monodon* is the more common type and practically all Pliocene mylagaulids have been referred to this species. It differs from the more distinctive Miocene forms by its large size, relatively large number of lakes, tendency of lakes to align themselves in rows, and by the fact that cement frequently forms an integral part of the wearing surface of the teeth (as in *Mesogaulus*). According to Matthew, the type of *M. monodon* is probably identical with *Epigaulus hatcheri*.

It is not practical to discuss here more fully the problems associated with the Mylagaulidæ. In many ways little is known about the group, and present knowledge has been summed up by various authors, principally by Matthew (1924). More specific discussion of a few of the problems has been presented in a paper dealing with the Rome, Oregon, rodent fauna (Wilson, 1937).

FAMILY APLDONTIIDÆ

The known history of the Aplodontiidæ extends from the upper Eocene to the Recent. However, aplodontids are relatively rare as fossils, and the post-John Day forms are limited to the middle Miocene *Liodontia*, middle Pliocene *Liodontia*, Pleistocene and Recent *Aplodontia*, and a single species from Asia, *Pseudaplodon asiatica* (lower Pliocene?).¹ In addition, a single upper premolar of an aplodontid is known from the Cedar Mountain region. Stirton (1932) has made the most recent determination on this specimen and regards it as representing *Meniscomys*, and as middle Miocene in age. It is more probable, however, that the specimen represents a Dp_4 of *Liodontia alexandræ* or closely related species, as suggested by C. L. Gazin (1932, p. 67), unless Stirton has obtained additional material from this locality.

The chief changes which took place between the middle Miocene and middle Pliocene were, in Pliocene forms: (1) mesostyles on upper teeth more acute, (2) reduction of ventral protuberance on lower

¹For a discussion of the relationships of this form, see the remarks at the end of this section.

jaws (approaching *Aplodontia*), (3) changes in development and position of masseter muscle (strongly developed and slightly farther forward, approaching *Aplodontia*), and (4) antero-external fold of lower molars more reduced. There was apparently no increase in size. (Gazin, 1932, pp. 63-67.)

Liodontia is usually assigned to a position intermediate between *Meniscomys hippodus* and the Quaternary *Aplodontia*. The later Tertiary form is distinguished from *Aplodontia* by the absence of a mesostylid on the lower molars of the former genus, and by an early reduction of the antero-external fold in the lower cheek-teeth. While *Liodontia* is certainly intermediate between the John Day and Recent aplodontids, it seems rather doubtful to the author that *Aplodontia* is a direct descendant of the Tertiary genus.

REMARKS ON THE ASIATIC RODENT *Pseudaplodon asiatica* (SCHLOSSER)

Max Schlosser in 1924 described what he believed to be an authentic record of a Tertiary (lower Pliocene?) aplodontid from Mongolia. The material, consisting chiefly of a lower jaw with dentition, was described as *Aplodontia asiatica*, new species. Later, Miller (1927) expressed doubt as to the affinity of this form with the aplodontids, suggesting that the animal represented a member of the dipodine group. At the same time, he erected the genus *Pseudaplodon* for the Asiatic form. Lastly, Gazin (1932) in his report on the Skull Spring mammalia of southeastern Oregon compared specimens of *Liodontia alexandrae* with Schlosser's species and suggested that the latter had separated from the aplodontid stock at a time when the development had reached a stage between *Meniscomys hippodus* and *L. alexandrae*. Gazin apparently did not doubt the aplodontid affinities of the Mongolian material, nor did he make any reference to Miller's views. However, he changed the original determination to *Aplodontia*(?) *asiatica*.

Perhaps a discussion of the affinities of *Aplodontia asiatica* lies beyond the scope of this paper, but the occurrence of an aplodontid in Mongolia, if substantiated, is of sufficient interest to justify a statement at this point. The taxonomic position of fragmentary rodent material, as Miller pointed out, is often extremely difficult to determine. In the present case even the scanty material is not at hand and only the original figures are available. It should be pointed out that Dr. Miller was aided in arriving at his conclusions by an examination of photographs which revealed some characters not clearly made out, or seen at all, in the published figures.

In support of his argument that *A. asiatica* is not related to the aplodontids, Miller presents the following points based on characters in the Asiatic species:

1. No mesostyle on cheek-teeth, whereas this is a fundamentally important structure in the aplodontids.

2. Small enamel lake near middle of crown in $P\bar{4}$, $M\bar{2}$, and $M\bar{3}$, obviously the last remnant of an infolding of enamel from the inner side of the crown. Such a re-entrant fold does not occur in *Aplodontia* at any age.

3. Presence of a broad, well-developed re-entrant angle on the anterior margin of crown of $P\bar{4}$, a region which in *Aplodontia* presents a smoothly rounded, forwardly directed convexity.

4. Anterior border of ascending ramus extends almost straight backward, and remains below the level of alveolar border to point where it is broken off, whereas in *Aplodontia* the anterior border of the ascending ramus curves up abruptly, high above the tooth-row from about the level of the second molar.

5. Part of jaw lying below the premolar is not deepened in the manner which is characteristic of *Aplodontia*.

6. Mandible shows a well-defined basin-like depression in the region between the hinder termination of the incisor (which is at level of space between $M\bar{2}$ and $M\bar{3}$, as in *Aplodontia*) and the base of the angular process. No such depression exists in *Aplodontia*.

7. Form of angular process is obviously different from that in the American animal, but neither the drawing nor the photographs represents this part of the jaw with adequate clearness.

With reference to the cheek-tooth characters stated by Miller, the following comments may be made from a study of the material from Skull Spring representing *Liodontia alexandræ*:

1. The mesostyle is indeed well developed in the aplodontids, but the corresponding structure in the lower grinders is absent in *Liodontia*.

2. Enamel lakes are present in the lower premolars of *L. alexandræ* until an advanced stage of wear. Two specimens of this species from Skull Spring exhibit lakes in $M\bar{3}$; another indicates the possible presence of a lake in $M\bar{1}$. Moreover, a study of John Day aplodontids shows that the presence of lakes certainly does not prohibit *A. asiatica* from having affinities with these animals.

3. A re-entrant angle at the anterior margin of $P\bar{4}$ is present at an early stage of wear in *L. alexandræ*.

Thus it seems that so far as dental pattern is concerned, there is apparently no valid reason for excluding the Mongolian species from the aplodontids. Comparison of characters in the ramus of *A. asiatica* with those of *Aplodontia* and *Liodontia* is difficult on the basis of Schlosser's figure and the material representing *Liodontia* which I have at hand. So far as the figure of *A. asiatica* is concerned, the ramus of that animal is not strikingly different from the corresponding

part in *Liodontia*, at least with regard to group separation. However, the photographs available to Miller show apparently major differences which prevent assignment of *A. asiatica* to any American aplodontid. Hence, the following comments involve considerably less valid objections to Dr. Miller's views than those on the dental characters.

4. If Miller is right in interpreting his photographs to mean that this character is not due to breakage of the jaw, it is a major difference separating the Asiatic form from either *Liodontia* or *Aplodontia*. However, most of the Skull Spring specimens are broken in this region, and this may be a rather common area of breakage. On this point difficulty may be encountered in an interpretation of even very clear photographs.

5. The deepening of the ramus below $P\bar{4}$ is not strikingly different from that in *L. alexandrae*, although the Skull Spring form may possess a slightly deeper jaw.

6. No remarks.

7. As far as Schlosser's figure is concerned, the angle is not very different from that in *Liodontia* and hardly seems to be of family importance, although Miller's photographs may show pronounced differences.

Conclusions—The dental characters stressed by Miller as separating *Aplodontia asiatica* from the aplodontids do not appear to be valid. Characters of the ramus seemingly prohibit an assignment of the species to any known genus of aplodontids. Although these characters may also exclude *A. asiatica* from relationship with the aplodontids, the agreement in dental pattern is such as to suggest this relationship rather than one with dipodine forms. In the latter group of rodents, so far as I know, there are no types which have dental patterns similar to that of *A. asiatica* and which also possess large lower premolars. In view of the geographic position of *A. asiatica*, its probable geologic age, and the character of the dental pattern, which Gazin has suggested is intermediate between *Meniscomys* and *Liodontia*, the generic name proposed by Miller is apparently valid. The Mongolian species is consequently designated as *Pseudaplodon asiatica* (Schlosser), and assigned to the Aplodontiidae as that family is defined in this paper.

FAMILY SCIURIDÆ

The Miocene has furnished more or less complete skulls of both *Sciurus* (tree-squirrel) and *Citellus* (ground-squirrel). The forms, as for example those recorded in the Skull Spring middle Miocene fauna, probably do not represent Recent *Sciurus* and *Citellus* in a strict sense. In a broad way, however, they do typify a differentiation into tree-squirrel and ground-squirrel groups.

No skulls or even fragments of skulls have been secured as yet from Pliocene beds. Hence our entire knowledge of the family for the Pliocene epoch is based on the dentition. Unfortunately, the dentition is extremely stable in the Sciuridæ. It is the little-modified descendant of the ancestral *Paramys* type, and in this respect is closer to the ancestral stock of the Rodentia than that of any other modern family of rodents. As a result, Pliocene sciurids offer little help in problems of correlation. Tree-squirrels and intermediate types of ground-squirrels that are fairly close to Recent forms are found in Pliocene strata. Some of the more specialized sciurids, such as *Marmota*, are also recorded. Noteworthy perhaps is the fact that no typical ground-squirrel of the genus *Citellus* has been recorded so far in strata older than the upper Pliocene. Hence the first appearance of these sciurids may be of value in correlation. However, until more complete phylogenies of the Sciuridæ are established, this fact is negative evidence and should be used with caution.

FAMILY CASTORIDÆ

Pliocene beavers appear to be represented only by the genera *Eucastor*, *Dipoides*, and *Castor*. These genera fall into two distinct phyla. Pliocene *Castor* represents the more primitive ancestor of the existing beaver (*Castor*), and *Eucastor-Dipoides* culminates perhaps in the Pleistocene giant beaver, *Castoroides*.

The earliest appearance of *Castor* on this continent may be in the upper Snake Creek and Rome middle Pliocene faunas. Members of the genus are not abundant, however, until the upper Pliocene. Pliocene *Castor* possesses distinctly shorter-crowned teeth than do Quaternary representatives of the genus, and with more complete material it may be found necessary to distinguish the former, at least in part, under a separate generic name. Somewhat similar forms in the Pliocene of Asia have been included in a distinct genus, *Sinocastor*, by Young. The direct ancestor of *Castor* is not found in North America, and Pliocene forms on this continent probably migrated here during this period. However, the lower Miocene *Palæocastor* is perhaps ancestral in a broad way to the line terminating in *Castor*.

Eucastor and *Dipoides* are successive types of an evolutionary series beginning with *Monosaulax* of the middle and upper Miocene and possibly leading to *Castoroides*. *Dipoides* is restricted apparently to the middle Pliocene in North America. *Eucastor* is characteristic of the lower Pliocene, although it is recorded also from the upper Snake Creek. Its presence in the middle Pliocene fauna may be the result of a reworking of the material evidence or of a mixing of specimens during collecting. An alternate explanation is that it is a survivor from the lower Pliocene.

Dipoides is distinguished from *Eucastor* by (1) a lengthening of the tooth-crown, (2) simplification of cheek-tooth pattern, and persistency of the simplified pattern (*i.e.*, resistance to the formation of lakes), and (3) larger size.

Possibly, as has been mentioned above, *Dipoides* in turn gave rise to *Castoroides*, since otherwise the Pleistocene genus stands in a strangely isolated position. This view has been advocated by Matthew, and more recently by Stirton. In support of this belief is the striking resemblance in cheek-tooth pattern, and continued increase in hypsodonty and size. However, *Castoroides* has been placed in a distinct family, the Castoroididæ, by Hay, Gidley, and others, on the basis of the quite noticeably modified skull. A skull of *Dipoides* described by Young (1927) appears to be fairly close to *Castor*. It might be added that although *Castoroides* shows an increase in size over *Dipoides*, this increase is tremendous. It is curious, therefore, that a beaver phylum in which the various species have been smaller than other castorids during most of its evolutionary history should suddenly give rise to the largest of all known beavers and the largest rodents of North America. Unfortunately, no upper Pliocene types are known which are related to either *Dipoides* or *Castoroides*, so that the descent of *Castoroides* cannot be definitely determined. Perhaps the fact that in some individuals of *Dipoides stirtoni* the fourth upper premolar possesses antero-external and internal inflections which are confluent, cutting through the narrow isthmus of dentine present in the more normal tooth (Wilson, 1934, pl. 1, fig. 4), foreshadows the character of the cheek-teeth in *Castoroides*.

Beaver types are known from the Valentine fauna (upper Miocene or Miocene-Pliocene?) which are intermediate between *Eucastor* and the Miocene *Monosaulax*. Typical *Monosaulax*, however, is less progressive than *Eucastor* with less hypsodonty in the cheek-teeth and more tendency to form isolated lakes. Until Stirton's work on the Tertiary beavers, *Monosaulax* was confused with *Palæocastor*, but the genus apparently is more closely related to the Old World *Steneofiber* than to North American palæocastors.

FAMILY HETEROMYIDÆ

All three Recent subfamilies of Heteromyidæ were in existence by lower Pliocene, namely the Perognathinæ (pocket-mice), Dipodomysinæ (kangaroo-rats), and Heteromyinæ (spiny pocket-mice). Representatives of the kangaroo-rats were not very clearly differentiated at this time, however, a fact which perhaps indicates that this group is not so important as a division of the family as are the other two. The only Recent genus of heteromyid in existence by the lower Plio-

cene is *Perognathus*, the most unspecialized of the modern genera in regard to dentition.

In contrast, during the upper Pliocene the only extinct genus so far recorded is *Cupidinimus*. Even the presence of this genus in the upper Pliocene is doubtful, although the form represented is not referable to any living genus.

Several aberrant lines are indicated by Pliocene heteromyid material. *Cupidinimus magnus* appears to be an aberrant kangaroo-rat, *Perognathoides* an aberrant pocket-mouse, and *Diprionomys* an aberrant heteromyine. Unfortunately, as is so often the case with fossil rodents, as well as larger mammals, only the approximate ancestors of Recent genera are known. Exception to this statement is seen in the Pliocene *Perognathus*, and possibly a genus (undescribed) from the Valentine fauna which is related to the Recent *Microdipodops*. The direct ancestors of the living spiny pocket-mice, *Heteromys* and *Liomys*, are not known.

The detailed evolution of the Heteromyidæ is too involved for discussion in the present paper. For further particulars, A. E. Wood's paper on the Heteromyidæ should be consulted (Wood, 1935).

Pliocene heteromyids are represented by the following genera:

Lower Pliocene

**Cupidinimus*, **Perognathoides*, **Diprionomys*, *Perognathus*

Middle Pliocene

**Cupidinimus*, **Diprionomys*, *Perognathus*

Upper Pliocene

?**Cupidinimus*, *Dipodomys*, *Perognathus*

* Genus extinct.

FAMILY GEOMYIDÆ

In spite of some determinations to the contrary, Pliocene gophers appear to be restricted to the group of true gophers of the subfamily Geomyinæ. The extinct group of the Entoptychinæ has been reported from the Pliocene in two occurrences. A single tooth from the Fish Lake Valley beds was referred by E. Raymond Hall to *Entoptychus*?. However, Hall pointed out that reference of the specimen to the Geomyidæ is doubtful, and, as has been mentioned, A. E. Wood has suggested that the specimen represents a lagomorph. Miss Louise Kellogg referred a specimen from the Thousand Creek to *Entoptychus minimus* new species. This species is congeneric with *Diprionomys* from the same locality, and perhaps specifically identical with *D. parvus*. In other words, it is a heteromyid and not a geomyid.

Lower and middle Pliocene gophers are in a state of considerable confusion. Some of these, as for example *Pliosacomys*, are far removed from Recent genera. The Recent forms, *Geomys* and

Thomomys, have been reported from the early Pliocene and even from the Miocene. It must be admitted that it seems quite likely that *Thomomys*, at least, was present by lower Pliocene time. On the other hand, no adequate description of any gopher material referable to a Recent genus and occurring in the lower and middle Pliocene has ever been published. Not a single specimen has been figured.

The first undoubted Recent genera are from the upper Pliocene, and *Geomys*, *Cratogeomys*, and *Thomomys* have been reported from this stage.

The genus *Pliosaccomys* from the early Pliocene appears to be a true geomyid, although a very primitive form for so late a stage in time. It is highly probable that this genus is aberrant, certainly so if *Thomomys* is actually present in the lower Pliocene. However, in the absence of any other types which are adequately known, it may be employed to suggest at least the main features of Pliocene evolution among gophers. The relationships of this form are discussed in a paper by the author on the Smiths Valley rodent fauna (Wilson, 1936).

Characters in *Pliosaccomys* together with certain features of the Recent genera, especially the character of unworn geomyid teeth, suggest that evolution in the Pliocene or at least the later Tertiary proceeded toward acquiring (a) persistent growth of crown, (b) differentiation of the enamel of the tooth-crown into discontinuous bands, and (c) more completely fossorial characters.

FAMILY CRICETIDÆ

The evolution of later Tertiary cricetids is very poorly known even for rodents. Only three genera have been recognized in the lower and middle Pliocene, and only one of these, the Recent genus *Peromyscus*, has any descendants in the upper Pliocene and Quaternary. Hence, observations on the evolution of the family during the Pliocene are limited to remarks on *Peromyscus* and a few statements concerning the relations of upper Pliocene cricetid species to Recent species.

The family Cricetidæ may be conveniently divided into two groups, the Cricetinae and the Microtinae. The former group is characterized by rooted molars whose crowns are normally brachydont and tubercular. There is a gradual transition to more flat-topped, prismatic teeth. The teeth are never rootless, however, and the posterior terminations of M₁ and M₂ are never angular. This group comprises the forms usually referred to as rats and mice (deer-mice, cotton-rats, wood-rats, and so forth). The Microtinae are characterized by possessing flat-topped, prismatic teeth, which are usually but not in-

variably rootless. The posterior terminations of M1 and M2 are angular. They are the voles and lemmings.

CRICETINÆ

Two genera of cricetines are known from the lower Pliocene, the Recent genus *Peromyscus* and *Macrognathomys*. The latter form is apparently aberrant and need not be considered further. *Peromyscus* is represented by a single species from Fish Lake Valley, *P. dentalis*. Compared with Recent species, it is characterized by low-crowned teeth and relatively unreduced third lower molars. It is much smaller than middle Pliocene members of the genus.

Peromyscus is the sole cricetine genus known from the middle Pliocene. Two species are present. Both differ from the lower Pliocene form in much larger size and higher-crowned teeth. They approach *P. dentalis* in possessing a relatively unreduced M3, and thus differ from upper Pliocene and Quaternary species, in which M3 is usually more reduced. The difference in size between lower and middle Pliocene forms is perhaps made more convincing by the fact that *Peromyscus* or *Peromyscus*-like species from the upper Miocene of the Barstow and Tonopah faunas are also much smaller than middle Pliocene forms. Thus it seems possible that the middle Pliocene was characterized by the existence of "gigantic" representatives of *Peromyscus*. The statement, of course, is not meant to imply that large types were the sole representatives of *Peromyscus* or *Peromyscus*-like forms at this stage, nor even that small forms only were present in the older or younger phases of the Pliocene. However, the known size distribution in time is suggestive, as is the fact that extremely large species of *Peromyscus* are now confined to quite southern regions.

In a strict sense, the genus *Peromyscus* probably does not exist previous to the upper Pliocene, and the earlier species should receive separate generic recognition. However, in view of the present state of our knowledge it is perhaps best to continue to refer these related types to *Peromyscus*.

The known upper Pliocene species of *Peromyscus* are relatively small forms with reduced third lower molars.

Upper Pliocene cricetines, in contrast to the preceding stages, are known by a number of rather diverse genera, all of which are still living. It is worth noting, however, that although the genera are living, the species are extinct.

Unfortunately, all of our upper Pliocene cricetines come from the Benson and Curtis faunas of the San Pedro Valley. Thus, not only do we know nothing of the upper Pliocene cricetines of other parts of

western North America, but the nature of the San Pedro Valley occurrence introduces doubt as to the exact age of the fauna from this area. In these assemblages we find the earliest record of *Sigmodon* (cotton-rat), *Onychomys* (grasshopper-mouse), and *Neotoma* (wood-rat). Moreover, *Eligmodontia* is likewise recorded from this locality. This genus is of interest since it is now limited to South America. Whether the Arizonan species was invading or leaving North America at that time is not known. It is not necessary to discuss the detailed characters which separate the upper Pliocene cricetines from their living relatives. The characters are minor ones but apparently distinct.

MICROTINÆ

Pliocene microtines are practically confined to the upper stage of the epoch. This statement has world-wide application at present. The earliest record of a microtine may be that of *Poamys* from the lower Snake Creek Miocene. Matthew has suggested that the genus is a structural ancestor. The genetic relationship of this genus to the microtines remains to be proved. The only other pre-upper Pliocene record is that of the genus *Goniodontomys* occurring in the Rome fauna of middle Pliocene age. Reference of this genus to the microtines is perhaps open to some doubt, but it seems closer to this group than to any other. *Goniodontomys*, if a vole, is an aberrant member of the group without descendants.

Certain upper Pliocene localities have yielded abundant, if incomplete, remains of Microtinæ. They are markedly less advanced than Recent types. In most of them, in comparison with Recent forms, there is a decided difference in tooth-pattern, less persistent growth of the cheek-teeth, and a lack of cement deposit on the teeth. Some upper Pliocene microtines are even distinct generically from Recent types. Both voles and lemmings are represented in the faunas. The latter are the only myomorphs with rootless teeth so far discovered in the North American Pliocene.

The microtine group has been used in Europe with marked success in correlation problems. Work on this group in North America also should prove valuable. These rodents may even furnish a means of zoning our upper Pliocene-Pleistocene, certainly a difficult task with most other groups of mammals. The Microtinæ also offer possibilities of intercontinental correlation, especially with regard to the genus *Mimomys*.

The following cricetids have been recorded from the Pliocene:

Lower Pliocene

Peromyscus, **Macrognathomys*

Middle Pliocene

Peromyscus, **Goniodontomys*

Upper Pliocene

Onychomys, *Sigmodon*, *Peromyscus*, *Eligmodontia*, *Neotoma*, ?*Neofiber*, *Synaptomys*, *Ondatra*, **Mimomys*

* Genus extinct.

It is evident from the above list that few of the upper Pliocene genera have any known ancestors in the earlier Pliocene. This point will be discussed later in some detail, as it has an important bearing on correlation of rodent faunas.

FAMILY ZAPODIDÆ

The only known North American Tertiary representative of the Zapodidæ is *Pliozapus* from the middle Pliocene of Smiths Valley, Nevada. Strangely enough at first sight, this genus is more closely related to the Recent Asiatic genus *Eozapus* than it is to either *Zapus* or *Napæozapus*, Quaternary representatives of the family on this continent. In cheek-tooth characters *Eozapus* is distinctly more primitive than either *Zapus* or *Napæozapus*, which explains to some degree its closer approximation to *Pliozapus*. *Pliozapus*, as represented by its single species *solus*, could hardly have given rise to *Eozapus*, as the species seems already too specialized. However, in most of its characters it is a good structural ancestor to the Asiatic type. If the Smiths Valley genus is ancestral also to Recent North American types, considerable evolution must have taken place in height of crown and more particularly in the development of the highly complex tooth-patterns of *Zapus* and *Napæozapus*. The ramus of *Pliozapus*, however, is quite close to that of Recent North American zapodids.

The North American ancestors of *Pliozapus*, if they are to be found on this continent, are quite unknown unless the Sespe Eocene *Simimys* proves to be a zapodid. *Protoptychus* from the Uinta and *Paciculus* from the John Day have both been referred by Hay to the Dipodoidea. A. E. Wood has suggested recently that *Paciculus* is a cricetid.¹ *Protoptychus* even if a dipodid cannot be more than distantly related to *Pliozapus*. Moreover, both *Protoptychus* and *Simimys* are so far removed in time from *Pliozapus* that, whatever their true relationships, they can have little real bearing on the problem of later zapodid evolution.

FAMILY ERETHIZONTIDÆ

Hystricomorphs are typically developed in South America, and all North American forms are invaders from that continent, or descend-

¹ A. E. Wood, Amer. Mus. Nov., No. 822, 4-5, 1936.

ants of those invaders. For this reason, no hystricomorphs are found in North America before the establishment of the later Tertiary union with the southern continent.

The first undoubted appearance of the group in North America is seen in the presence of the extinct species *Erethizon bathygnathum* in the upper Pliocene Grand View fauna. The principal differences between this species and living North American porcupines are in the heavier jaw and slightly different tooth proportions.

The first appearance of hystricomorphs on this continent should furnish an important marker when the date is definitely established. South American sloths have been found in our faunas as early as the upper Snake Creek and Rattlesnake, so that it is not certain that the upper Pliocene marks the first appearance of southern rodents in North America. Moreover, *Hystricops* Leidy (upper Miocene?) has been referred at various times to the beavers and to the porcupines. Stirton considers this genus a castorid.

FAMILY CAVIIDÆ

Types related to the living giant capybara of South America are found in the Pleistocene faunas of North America. So far, none of these forms has been recorded from the Pliocene.

FAMILY OCHOTONIDÆ

As has been mentioned previously, the lagomorphs are not rodents in a strict sense. Since, however, the order Lagomorpha is so restricted and compact, and since it is usually associated with rodents in a popular sense, both groups are included in the present paper.

The lagomorph family Ochotonidæ or pikas have not been definitely recorded in the Pliocene. The presence of an aberrant ochotonid in the Virgin Valley middle Miocene fauna and the occurrence of *Ochotona* in the Recent fauna implies their presence in the Pliocene. Perhaps undescribed pikas are in existence in Pliocene lagomorph collections but have been confused with leporids.

FAMILY LEPORIDÆ

No definitely observable evolutionary changes take place in Pliocene Leporidæ. The genera include **Hypolagus*, *Sylvilagus?*, **Akilepus?*, *Lepus*, and *Sylvilagus* or *Brachylagus*. *Hypolagus* is the most important Pliocene genus, and *Lepus* deserves mention because of stratigraphic problems attached to its first appearance in North America. The remaining genera are of minor importance and will not be mentioned further.

The generic status of *Hypolagus* has long been a subject of considerable debate. Matthew always held to the view that there was not

sufficient evidence to warrant its recognition as a distinct genus. However, later work with additional material and the general tenor of the evidence suggest that *Hypolagus* is entitled to generic rank. Moreover, distinct or not in a strict taxonomic sense, the genus is distinguishable from *Lepus*, and there is little evidence to indicate that it ever gave rise to the Recent *Lepus*.

Hypolagus and *Lepus* have never been found in association in the Pliocene of North America, and the only fauna in which this occurs is the lower(?) Pleistocene Anita, Arizona, assemblage. In this case the species of *Hypolagus* present in the fauna may not be a typical *Hypolagus*. This is the last appearance of the genus.¹ The earliest record of *Lepus* in North America is in the Benson and Curtis faunas of San Pedro Valley, Arizona.

The present author regards true *Lepus* as probably an emigrant from Asia and believes that its appearance in North America brought about a rapid extinction of *Hypolagus*. Dr. Dice (1929, pp. 343-344) appears to have indirectly suggested this same view. Moreover, if this is true, *Lepus* seems to have arrived at about the opening of the Pleistocene as defined in this paper, and faunas in which *Hypolagus* but not *Lepus* is present are older than faunas in which the modern genus is a member. According to this view, the Grand View and Hagerman faunas are older than the San Pedro Valley faunas, if *Lepus* is actually a member of these assemblages. Since the statement that the San Pedro Valley assemblages are younger than those from Grand View and Hagerman is probably not countenanced by many or any American palæontologists at present, a fuller discussion will be presented in a later section of this paper.

ANALYSIS OF PLIOCENE RODENT FAUNAS

The following lists are in part a repetition of those already given. They are repeated for the sake of clearness in the presentation of the following sections. Most of the doubtful genera have been omitted. Likewise genera which are undoubtedly present (for example *Liodontia* in the lower Pliocene), but have not been definitely recorded, are also omitted. The latter omission is made in order to give ratios of sciurormorphs to myomorphs without including genera that have not actually been found. Disposition of the Valentine fauna and of

¹L. R. Dice has referred *Lepus giganteus* Brown from the Conard Fissure to *Hypolagus*. The type and only known specimen is a fragment of skull with P3 and P4. Recently C. Bertrand Schultz has referred a lagomorph jaw from the middle(?) Pleistocene of Nebraska to this species, retaining the original generic designation (Nebr. State Mus., vol. 1, bull. 41, 1934). The type specimen hardly seems adequate for definite assignment to *Hypolagus*. Apparently Dice based his determination on the fact that in *L. giganteus* the enamel re-entrants of the cheek-teeth extend only slightly more than half-way across the occlusal surface. In *Lepus* these re-entrants extend about three-quarters of the distance across the tooth.

other assemblages in which the age of the forms is doubtful has been somewhat arbitrary. For instance, *Cupidininus nebraskensis* has been omitted because of possible Miocene age. Balancing this omission to a certain extent is the inclusion of *Diprionomys* on the evidence of its presence in the Devil's Gulch beds. In view of the uncertain systematic position of *Kansasimys*, this genus has been excluded from consideration.

LOWER PLIOCENE

Order Rodentia

*Family Ischyromyidae

None

Family Aplodontiidae (North America and Asia)

None recorded

*Family Mylagaulidae (North America)

Mylagaulus*Epigaulus*

Family Sciuridae (practically world-wide distribution)

None recorded

Family Castoridae (Northern Hemisphere)

**Eucastor*

Family Heteromyidae (North and Central America; northern part of South America)

Perognathoides*Diprionomys*

Family Geomyidae (North and Central America)

None recorded?

Family Cricetidae (practically world-wide distribution)

*Peromyscus***Macrogathomys*

Family Zapodidae (North America and Eurasia)

None

Family Erethizontidae (North and South America)

None

Family Caviidae (South America; Pleistocene of North America)

None

Order Lagomorpha

Family Ochotonidae (Holarctica)

None recorded

Family Leporidae (practically world-wide distribution)

**Hypolagus*

* Genus extinct.

Lower Pliocene extinct genera.....	7
Lower Pliocene living genera	1
Lower Pliocene sciuromorph genera	5
Lower Pliocene myomorph genera.....	2
Lower Pliocene hystricomorph genera	0

If lower Pliocene genera that are known to be present but have not been recorded so far are added to the above list, the predominance

of sciuiromorphs over myomorphs is increased to five to one. The number of types is not sufficiently large to permit this ratio to mean much in a numerical sense, but it is nevertheless true that the sciuiromorphs greatly outnumber the myomorphs. Practically all known lower Pliocene rodents represent extinct genera. Even *Peromyscus*, in the above list, is probably generically distinct from the living form. The only living North American genera which very likely extend back without generic change to the lower Pliocene are *Perognathus*, *Sciurus*, *Citellus* (in the broad sense), and possibly *Thomomys*.

It should be noted that there is no decided faunal break between the upper Miocene and lower Pliocene faunas. None of the lower Pliocene genera appears to be an introduced type, and the entire fauna evolved from existing North American Miocene forms. Probably the only very distinctive rodent type for this stage is *Eucastor*.

The lower Pliocene rodent faunas may be characterized as follows:

1. Great preponderance of sciuiromorphs over myomorphs.
2. High percentage of extinct genera.
3. No strikingly new or introduced types.
4. Presence of the genus *Eucastor*.

MIDDLE PLIOCENE

Rodentia	Family Geomyidæ
*Family Ischyromyidæ	* <i>Pliosacomys</i>
None	<i>Thomomys</i>
Family Aplodontiidæ	Family Cricetidæ
* <i>Liodontia</i>	* <i>Goniodontomys</i>
*Family Mylagaulidæ	<i>Peromyscus</i>
* <i>Mylagaulus</i>	Family Zapodidæ
Family Sciuridæ	* <i>Pliozapus</i>
<i>Sciurus</i>	Family Erethizontidæ
<i>Citellus</i>	None
<i>Marmota</i>	Family Caviidæ
Family Castoridæ	None
* <i>Dipoides</i>	Lagomorpha
<i>Castor</i>	Family Ochotonidæ
Family Heteromyidæ	None recorded
* <i>Diprionomys</i>	Family Leporidæ
* <i>Cupidinihus</i>	* <i>Hypolagus</i>
<i>Perognathus</i>	
* Genus extinct.	
Middle Pliocene extinct genera.....	9
Middle Pliocene living genera	7
Middle Pliocene sciuiromorph genera	12
Middle Pliocene myomorph genera	3
Middle Pliocene hystricomorph genera	0

Because of the large number of known middle Pliocene genera, the sciuiromorph preponderance over the myomorphs is more striking.

There are relatively fewer extinct genera. The ratio of living to extinct genera during this stage is about one to one. Several introduced or at least distinctly new types are present, namely, *Castor*, *Goniodontomys*, and possibly *Pliozapus*. The introduction of the true beaver phylum (*Castor*) from the Old World is fairly well established. Moreover, the only beavers that appear to be related to *Castor* and are older than middle Pliocene are Old World types. The microtine genus *Goniodontomys* may also have an Old World background. It is usually agreed upon that the Old World was the seat of higher myomorph evolution, but it should be pointed out that no microtine older than, or as old as, *Goniodontomys* has ever been found there. If *Poamys* from the lower Snake Creek can be shown to be approximately ancestral to the Microtinæ, this continent may after all be the site of evolution of some of the higher Myomorpha. *Pliozapus* may also be an introduced type, but it seems possible that North America was the place of evolution of the Zapodinæ. The most distinctive middle Pliocene rodent is the beaver genus *Dipoides*. *Dipoides* appears to be characteristic for the mid-Pliocene everywhere in North America. It should be noted that the Mylagaulidæ become extinct with the close of this stage. It has already been pointed out that large species of *Peromyscus* are characteristic of the middle Pliocene.

Middle Pliocene rodent faunas may be characterized as follows:

1. Great preponderance of sciuromorphs over myomorphs.
2. Approximately equal number of extinct and living genera represented.
3. Introduction of *Castor* in later faunas.
4. First appearance of Microtinæ.
5. Presence of "gigantic" *Peromyscus*.
6. Presence of the genus *Dipoides*.
7. Last appearance of the mylagaulid rodents.

So far nothing has been said concerning conclusions which may be drawn with reference to the ecologic conditions under which the various faunas lived, and which prevailed in general during the lower and middle Pliocene. Most of our rodent faunas are too incomplete to draw any very definite conclusions. Moreover, although we know a great deal about the ecology of living rodents, the application of this knowledge to fossil forms becomes increasingly uncertain as we go back in geologic time. In all probability forms which at present are restricted to certain types of environment enjoyed a wider field in the past. In addition, many genera of living rodents occupy a wide range of environments even though particular species or races are sharply restricted. Hence the presence of a related type in the Pliocene does not often suggest definite living conditions. However, in many Pliocene rodents there is an increase in hypsodonty in middle Pliocene

forms over those of the lower. The suggestion may be made that this is in response to the increasing aridity which occurred with the passing of Pliocene time, a response which culminated in the upper Pliocene in the appearance of many of our Recent genera with long-crowned teeth.

UPPER PLIOCENE

Rodentia	Family Cricetidæ
*Family Ischyromyidæ	<i>Peromyscus</i>
None	<i>Onychomys</i>
Family Aplodontiidæ	<i>Sigmodon</i>
None recorded	<i>Eligmodontia</i>
*Family Mylagaulidæ	<i>Neotoma</i>
None	<i>Synaptomys</i>
Family Sciuridæ	<i>Ondatra</i>
<i>Citellus</i>	* <i>Mimomys</i>
Family Castoridæ	Family Zapodidæ
<i>Castor</i>	None recorded
Family Heteromyidæ	Family Erethizontidæ
* <i>Cupidini</i> ?	<i>Erethizon</i>
<i>Perognathus</i>	Family Caviidæ
<i>Dipodomys</i>	None recorded
Family Geomyidæ	Lagomorpha
<i>Thomomys</i>	Family Ochotonidæ
<i>Geomys</i>	None recorded
<i>Cratogeomys</i>	Family Leporidæ
	* <i>Hypolagus</i>
	* <i>Alilepus</i> ?
	<i>Lepus</i>

* Genus extinct.

Upper Pliocene extinct genera.....	4
Upper Pliocene living genera.....	16
Upper Pliocene sciuromorph genera.....	8
Upper Pliocene myomorph genera.....	8
Upper Pliocene hystricomorph genera.....	1

For the first time in the Tertiary of North America, myomorphs form an important element in the fauna. The ratio given above of one to one is probably in large measure accidental, but that there is a relative increase of myomorph genera cannot be doubted. A decrease of sciuromorph genera is also indicated, but this is fortuitous. Undoubtedly all Recent genera of Sciuromorpha were in existence by the end of the Pliocene, which would at least double the number indicated above.

An idea of the expansion of the myomorph element may be gained by recalling that all eight of the listed genera belong to one family, the Cricetidæ. The same family in the middle Pliocene has only two recorded representatives. Not only do the myomorph genera increase in number between the middle and upper Pliocene, but the number of

known specimens increases even more. Four myomorph genera are known from the lower and middle Pliocene. Of these, three are extinct and one living. The extinct genera are represented by a total of only four specimens. I do not know how many specimens of myomorphs are actually available from the lower and middle Pliocene, but from those I have seen, an estimate of less than two dozen would be warranted. Moreover, most of this material represents *Peromyscus*. The number of specimens in the California Institute collection of one upper Pliocene species alone, *Mimomys? parvus*, exceeds this figure. A specimen of *Mimomys* has even been found in an oil-well core. It must be remembered of course that most myomorphs are tiny animals, smaller than the average sciuromorph. It is natural to assume that these forms have often been overlooked in collecting. Also, the point should be raised that the small number of earlier Pliocene myomorph genera results from the limited amount of material available. Conversely, it might be argued that the larger number of upper Pliocene forms is directly due to the increased amount of material recovered from beds of this age. However, a number of small sciuromorphs have been found, and the factor of size would have little influence on the number of specimens of pre-upper Pliocene myomorphs as compared with upper Pliocene and Pleistocene types. In many cases the same individuals have made the collections from each of the horizons, and the collecting technique may be assumed to be approximately the same.

If, as it appears, therefore, a decided expansion of myomorph types occurred in upper Pliocene time, this fact may be employed in distinguishing the rodent faunas of the upper Pliocene from those of other stages of the Pliocene. The expansion is probably due to a combination of evolution and of migration from other regions.

The generally high percentage of sciuromorphs in the early Pliocene rodent faunas of North America stands in decided contrast to that in the faunas from the two adjoining continents, South America and Asia. The former continent possessed throughout the Pliocene an almost exclusively hystricomorph fauna. The Asiatic faunas, more particularly those of northern China and Mongolia, show a decided myomorph representation. The following rodent list from the upper Miocene and early Pliocene of Mongolia and northern China is given for comparison with the North American early Pliocene faunas. Some of the forms in this list are incorrectly determined, but this is relatively unimportant, since the purpose is to show the contrast in the major details of the fauna between Asia and North America. It is also possible that some upper Pliocene genera are included in this list. Genera that appear too doubtful have been omitted.

ASIA (UPPER MIOCENE AND EARLY PLIOCENE)		NORTH AMERICA (EARLY PLIOCENE)	
Sciuromorpha		Sciuromorpha	
<i>Pseudaplodon</i>		<i>Mylagaulus</i>	
<i>Tamius?</i>		<i>Epigaulus</i>	
<i>Castor</i>		<i>Liodontia</i>	
<i>Dipoides</i>		<i>Sciurus</i>	
Myomorpha		<i>Citellus</i>	
Jerboas		<i>Marmota</i>	
<i>Paralactaga</i>		<i>Eucastor</i>	
<i>Protalactaga</i>		<i>Dipoides</i>	
<i>Alactaga?</i>		<i>Castor</i>	
<i>Plesiodipus</i>		<i>Perognathus</i>	
Sicistids		<i>Perognathoides</i>	
<i>Heterosminthus</i>		<i>Diprionomys</i>	
Cricetids		<i>Cupidinimus</i>	
<i>Sinocricetus</i>		<i>Thomomys</i>	
<i>Lophocricetus</i>		<i>Pliosaccomys</i>	
<i>Microtodon</i>		Myomorpha	
Gerbillinæ		<i>Pliozapus</i>	
<i>Gerbillus</i>		<i>Peromyscus</i>	
Cape Rats		<i>Macrogathomys</i>	
<i>Prosiphneus</i>		<i>Goniodontomys</i>	
<i>Siphneus</i>			
Murines			
<i>Acomys?</i>			
Rhizomyidæ			
<i>Pararhizomys</i>			
Sciuromorph genera	4	Sciuromorph genera	15
Myomorph genera	13	Myomorph genera	4
Hystricomorph genera	0	Hystricomorph genera	0

A second distinctive feature of the upper Pliocene rodent faunas of North America as compared with earlier assemblages of the Pliocene lies in their modernization. Very few extinct genera are recorded, and, excepting the lagomorphs, even these are fairly close to modern types.

A number of upper Pliocene genera have no immediate ancestors in the North American Pliocene. Such genera are: *Sigmodon*, *Neotoma*, *Erethizon*, *Lepus*, *Alilepus?*, the microtine genera, and possibly *Eligmodontia*.

Pliocene *Sigmodon*, *Neotoma*, and *Eligmodontia* are found only in the San Pedro Valley fauna. It should be noted that this fauna has the most southerly position of any of the Pliocene rodent assemblages. Moreover, the above-named genera have at present a pronounced southern distribution. This statement is not true of *Neotoma*, but the genus is one of a number of genera which have such a distribution and are sometimes included in a separate subfamily, the Neotominae. Several extinct South American rodents have also been included in

this group. It is doubtful whether the Neotominæ originated in any very southern locality, since the time available does not seem sufficient for an ancestral stock of the Neotominæ to have migrated southward and then returned. However, some such event may in part account for the lack of immediate ancestors of *Neotoma* in the early Pliocene of North America.

A species of *Sigmodon*, namely *atavus*, has been described by Schlosser (1924) from Mongolian Pliocene? beds. G. S. Miller (1927, pp. 17-19) stated that this supposed occurrence is an error and made Schlosser's species the type of a new genus, *Microtodon*, without affinities with *Sigmodon*. This view is more nearly in accord with the distributional evidence, and *Sigmodon* is probably to be considered an offshoot from some American *Peromyscus*-like stock.

The present southern distribution of *Eligmodontia* has been mentioned. The genus is sufficiently close to *Peromyscus* to have been derived from this form or its immediate predecessors before migration to South America, but what actually occurred is not known.

Erethizon is an undoubted derivative of a South American stock. The first appearance of the family in North America may be of considerable importance in Pliocene correlation.

Lepus and *Alilepus*, if the latter is properly referred to the Asiatic genus, were invaders from Asia. It seems likely that *Alilepus* was an earlier arrival than the modern hare. The first appearance of *Lepus*, in the author's opinion, is very close to the beginning of the Pleistocene as that period is defined in this paper.

The earliest undoubted record of *Lepus* in North America is in the San Pedro Valley faunas. *Lepus* can hardly be considered a derivative of *Hypolagus*, and presumably invaded this continent from the north during the later Cenozoic. The rapid extinction of *Hypolagus*, consequent upon the appearance of *Lepus*, is supported by the fact that in only one known fauna, the Anita, of lower(?) Pleistocene age, is there any association of the two genera. The Grand View assemblage is either latest Pliocene or Pleistocene. Equine remains from this fauna are very close to *Equus* and perhaps could be assigned as well to that genus as to *Plesippus*. *Hypolagus* is a member of this fauna, but no remains of *Lepus* are known. If *Lepus* had already arrived on this continent it should be recorded in this fauna, since the latter occupies a geographic position far to the north of the San Pedro Valley assemblages. If the Grand View assemblage is considered alone, the absence of *Lepus* may not possess great significance. However, the presence of *Hypolagus* and the absence of *Lepus* in the related Coso Mountains and Hagerman faunas strengthens the view that these assemblages antedate the appearance of *Lepus*. In this connection, the present wide distribution of *Lepus* should be borne in

mind. Judging from the almost universal presence of *Hypolagus* from the middle Miocene to upper Pliocene of the Great Basin and Pacific Coast provinces, the genus had a range approximately like the present distribution of *Lepus* in North America. It thus seems reasonable to suppose that the San Pedro Valley faunas, on the basis of lagomorph remains, are younger than that from Grand View.

It is of interest to note that Th. Kormos has recorded the genus *Hypolagus* from the Hungarian upper Pliocene (Kormos, 1934). In younger but still Pliocene strata, *Hypolagus* is found in association with sporadic occurrences of *Lepus*. In deposits containing still younger faunas, *Lepus* gradually replaces the more primitive form. Apparently no transitional types are known between the two genera. However, in Hungary *Hypolagus* seems to have prevailed somewhat later than in North America, unless the record results from a fuller European sequence of strata.

The San Pedro Valley fauna has been divided into two parts, an earlier fauna, the Benson, and a later one, the Curtis. *Lepus* is recorded in both. J. W. Gidley regarded the Benson fauna as of upper Pliocene age and slightly older than the Blanco; the Curtis fauna as slightly younger (Gidley, 1926, p. 83). Unfortunately, the only detailed descriptions of these faunas are of the rodents, lagomorphs, edentates, and proboscideans. Other forms have received only preliminary mention. Gidley records the presence of true *Equus*, *Lama*, Cf. *Pliauchenia*, Cf. *Procamelus*, *Odocoileus*, *Merycodus*, *Stegomastodon*, and *Glyptotherium* from the Curtis fauna. The Benson assemblage includes *Pliohippus*, *Hipparion*, Cf. *Pliauchenia*, Cf. *Procamelus*, *Platygonus*, *Merycodus*, and *Anancus*. It should be recalled that both faunas occupy apparently the same stratigraphic position in the San Pedro Valley beds. The Curtis fauna possesses some forms which may be Pleistocene. The anomalous presence of *Merycodus* and of other types suggests that there has been a reworking of the material in the deposit, and that part of the fauna is indeed Pleistocene, thus agreeing with the evidence furnished by the presence of *Lepus*. If this is true for the Curtis locality, a similar circumstance may account for the presence of *Lepus* in the Benson fauna. Accordingly, the view might be held that two faunas are present, an upper Pliocene assemblage equivalent to or slightly older than the Blanco, and a Pleistocene fauna. I have not examined material from the Benson locality, but that of the Curtis fauna in the California Institute collections is very fragmentary and is not incompatible with the view of reworking. However, the rodent faunas from the two localities indicate no great separation in time. Moreover, Gidley's description of the occurrence and the rather complete preservation in some cases seemingly argue against any mixing on a large scale.

In view of their southerly location, the San Pedro Valley faunas may appear slightly older than they actually are. This suggestion, however, is again inadequate to explain entirely the stage of evolution presented by some of the forms. The author, of course, is here concerned only with the presence of *Lepus* in the faunas. The Rodentia could be upper Pliocene, but not older. Perhaps the hares are not typical members of either fauna and have been introduced by some means not determined.

The final solution of the problem offered by the San Pedro Valley faunas must await detailed description of the remaining elements of the assemblages, which may alter the present determinations to some extent, and perhaps more detailed geologic examination of the beds. For the present, the faunas present an obstacle to the acceptance of the view that *Lepus* is exclusively Pleistocene in age.¹

SUMMARY OF UPPER PLIOCENE RODENT FAUNAS

The principal characteristics of upper Pliocene rodent faunas are as follows:

1. Sharp faunal break from the middle Pliocene as evidenced by: (a) decided increase in myomorph population; (b) decided decrease in number of extinct genera; (c) first appearance of many modern types.
2. No Mylagaulidæ.
3. Presence of the genus *Mimomys*, as well as the relative abundance of microtines.
4. No *Dipoides*, nor at present any known representative of the *Eucastor-Dipoides* line.
5. Absence of *Lepus*, except perhaps in final(?) faunal stages.
6. First appearance of typical *Citellus*.
7. First appearance of hystricomorphs(?).
8. All species probably extinct.

ECOLOGY OF UPPER PLIOCENE FAUNAS

The Grand View, Hagerman, Benson, and Curtis faunas are the only upper Pliocene rodent assemblages complete enough to afford much evidence as to the ecologic conditions during the upper Plio-

¹Since the present report was written I have been informed by Dr. C. L. Gazin that *Hypolagus* is present in the Benson fauna. This information caused me to realize that I had been uncritical in accepting Dr. Gidley's identification of the Benson lagomorphs. A reinvestigation of the fauna suggests that specimen No. 10529, or at least a P3 referred to this number, identified by Gidley as *Sylvilagus* or *Brachylagus* sp., represents a *Hypolagus*. Moreover, the specimens referred to *Lepus* are hardly adequate to demonstrate definitely the presence of jack-rabbits in the Benson assemblage. However, *Lepus* is present in the Curtis fauna, and the rodent and lagomorph assemblages from the Benson and Curtis localities apparently are sufficiently related so that the above discussion is not rendered pointless by any changes in identification which may be made in the future.

cene. These faunas fall into two groups both geographically and ecologically. The Grand View and Hagerman faunas suggest the close proximity of fresh water and the general prevalence of rather moist conditions with abundant grasses. Moreover, the presence of voles and especially of lemmings indicates perhaps a relatively cool climate. Lemmings in general point to a boreal climate. Hence their presence in the Grand View fauna might suggest proximity to the Glacial Period or to a time of actual glaciation of the continents. It must be pointed out, however, that *Synaptomys* extends today into the upper Austral zone, its range reaching as far south as North Carolina, Tennessee, and Arkansas. Further, its range may have been less restricted in the upper Pliocene. The Benson and Curtis faunas, on the other hand, suggest, in the presence of *Dipodomys*, *Onychomys*, and *Perognathus*, assemblages that existed under arid or semiarid conditions. The presence of *Sigmodon* and *Neofiber?* suggests that areas of a moister environment were also present. On the whole, the Grand View and Hagerman assemblages point to a cool, rather moist climatic condition, and the San Pedro Valley fauna to a warm, drier environment.

During the earlier Pliocene there was a gradual increase in hypsodonty of the cheek-teeth in many rodent types. This change seems to be abruptly accelerated in the upper Pliocene. The coming of glacial conditions may account for the appearance of such forms as the microtines, and the increasing aridity for the appearance of *Dipodomys* and similar types.

CORRELATION OF PLIOCENE RODENT FAUNAS

It should be indicated at the outset that the correlations made in this section are tentative. Many of the rodent faunas are small and incompletely known. Faunas of identical age may have few or no forms in common as a result of varying environmental conditions or of fortuitous collecting, since the Rodentia show great differentiation. It would be quite surprising if all the exact correlations were correct. Perhaps such correlations, in view of the scanty evidence, should not be made. However, in some cases the larger mammals associated with the rodents have not been studied in detail and the relative position of the fossil assemblages is not known. Hence, if in the last analysis the attempted correlations are proved correct, the fact may demonstrate the value of fragmentary remains of rodents in determining stratigraphic relationships.

It seems fairly well established that the known Pliocene rodent faunas may be divided primarily into three groups corresponding in age to the lower, middle, and upper divisions of the Pliocene as recognized in this paper. The characteristics of these stages have been set forth in the preceding section. A fourth and youngest stage, charac-

terized by the presence of *Lepus*, may also be present. If this actually exists, it might best be referred to the lower Pleistocene.

Not enough attention has been given in recent years to the Pleistocene rodent assemblages to furnish a basis for recognition of faunal stages within this epoch. If valid inferences are to be drawn from what is known, as well as from the character of the upper Pliocene fauna, the lower Pleistocene should be characterized by (1) the presence of *Lepus* among the lagomorphs, and (2) the presence of principally extinct species, readily recognizable as such. This stage is possibly represented by one or both of the San Pedro Valley faunas, and the Anita, Arizona, fissure accumulation described by Hay (1921). Theoretically, at least, the middle Pleistocene should yield a mixture of living types of rodents and those definitely extinct. Some of the eastern wet-cave faunas appear referable to this age. Recently, Lugin and Schultz (1934) have referred the "Sheridan beds" and the Hay Springs Quarry fauna tentatively to the middle Pleistocene. Upper Pleistocene rodent faunas comprise only existing species, or if any are extinct they are closely allied to living forms. However, exception to this statement must be made if the genus is extinct, as may be the case whenever the aberrant *Castoroides* is present. The most completely known upper Pleistocene assemblages are those of the California tar-pits. The age of the tar-pit faunas has been a subject of much discussion. At first, Rancho La Brea was regarded as representative of the Aftonian interglacial stage. Later work has tended to transfer this assemblage to the upper Pleistocene, and the rodent faunas of this and similar occurrences strongly suggest also a late stage in Pleistocene time.

If some or all of the more typical upper Pliocene faunas are eventually placed in the Pleistocene, this will serve only to move up the Pleistocene faunas without changing their relative positions. In this event, the first appearance of *Lepus* in the faunas would not coincide with the beginning of the Pleistocene but with a later but still lower Pleistocene stage.

Certain Pliocene rodent faunas have been omitted from the discussion either because they are very fragmentary or because the present author is not familiar with them. The following assemblages are discussed in this section: Fish Lake Valley, Siesta, Kern River, Rattlesnake, Rome, Smiths Valley, Thousand Creek, upper Etchegoin, Coso Mountains, Hagerman, Grand View, Benson, and Curtis. These faunas fall more or less readily into one or another of the three main faunal stages established in this paper.

LOWER PLIOCENE

The Siesta and Fish Lake Valley rodent faunas are characteristic of the lower Pliocene. The Siesta is so poorly known that it would be

omitted except for the fact that the beds furnish material representing *Eucastor*, one of the most useful rodent types in Pliocene correlations. The species, *E. lecontei*, is clearly more advanced than that from Fish Lake Valley, and less advanced than *Dipoides* from the middle Pliocene. For this reason the Siesta is placed above the Fish Lake Valley fauna and below the mid-Pliocene assemblages.

The Fish Lake Valley or Esmeralda fauna is the most primitive of the rodent faunas dealt with in this section. Not only is it characterized by the most primitive known species of *Eucastor*, but *Peromyscus dentalis*, from this fauna, is distinctly more primitive than mid-Pliocene species. Moreover, the Fish Lake Valley heteromyids appear to be closely related to forms from the Barstow. The fauna would be considered Miocene by some palæontologists. The author has no preference in the assignment of this assemblage to either the lower Pliocene or the upper Miocene, but the appearance of the genus *Eucastor* is a convenient Pliocene marker. The Equidæ from the Fish Lake Valley fauna include the genus *Hipparion*, which is still considered a "signpost" of the Pliocene by most workers.

MIDDLE PLIOCENE

The following faunas appear to be of middle Pliocene age: Rattlesnake, Kern River, Smiths Valley, Thousand Creek, and Rome. The relative position of these faunas with regard to one another is uncertain.

A species of *Dipoides* is recorded from the Rattlesnake. This species is apparently less advanced than *D. stirtoni* of the Rome fauna. For this reason, the Rattlesnake is considered as slightly older than the Rome rodent fauna. The scarcity of rodent material, including that of *Dipoides*, in the Rattlesnake collections prevents any very reliable age determination on the basis of the Rodentia. If the Rome rodent assemblage is at least as advanced as that from Thousand Creek, then the available material from the Rattlesnake supports the general opinion that the Rattlesnake is somewhat older than the Thousand Creek.

The Thousand Creek rodents comprise the largest and most complete assemblage among the middle Pliocene faunas. Fragmentary remains of *Dipoides* represented in the assemblage may be identical with *D. stirtoni*, but it is impossible to make this determination with certainty. A large species of *Peromyscus*, *P. antiquus*, is also recorded. The Thousand Creek rodent fauna may be slightly older than that from Rome. This is suggested by the presence in the latter of *Castor* and a microtine genus, *Goniodontomys*. These forms are more characteristic of the upper than of the middle Pliocene, and perhaps point to a younger age for the Rome fauna. However, these animals

are rare in the Rome collection, and their absence in that from Thousand Creek may be fortuitous or due to the presence of somewhat different environmental conditions. Study of the Rome assemblage as a whole has not been extended sufficiently to determine the exact relationships of this fauna other than to establish for it an age comparable to that of the Rattlesnake-Thousand Creek.

The Smiths Valley rodent fauna is tentatively regarded as approximately contemporaneous with, or slightly older than, the Thousand Creek fauna. Practically identical species of *Peromyscus* are found at both localities. The cotype of *Cupidinimus magnus* from the Thousand Creek exhibits a certain resemblance to the Smiths Valley *Pliosaccomys*. If specific identity could be established, similarity of the two faunas would be strengthened. However, the relation of these rodent types cannot be satisfactorily determined with the existing Thousand Creek material. As a matter of fact, they are referred to separate families.

No especially diagnostic forms are known from the Kern River. Presence of a large species of *Peromyscus* is regarded by the author as indicative of a middle Pliocene age. Owing, however, to the incomplete character of the rodent remains, an age assignment to this fauna becomes largely dependent upon evidence furnished by the larger mammals. As a matter of fact, owing to the fragmentary nature of most rodent faunas, more or less use is made of other lines of evidence in arriving at age determinations. If rodent assemblages offer evidence concerning relative ages of faunas, I have not hesitated to use this in preference to other data, but in its absence I have fallen back on the usually accepted testimony of the larger mammals.

UPPER PLIOCENE

The upper Pliocene rodent faunas included in this discussion are: upper Etchegoin, Coso Mountains, Hagerman, Grand View, Benson, and Curtis. The latter four are the only faunas of any considerable size. Unfortunately, the Hagerman-Grand View faunas differ so much in type from the Benson-Curtis assemblages that comparisons are quite limited. I have placed the Idaho faunas as slightly older than those from Arizona, chiefly because the latter are characterized by the presence of *Lepus*, the former by *Hypolagus*.

The Grand View mammalian assemblage appears to be slightly younger than that from Hagerman. Rodent forms suggesting this difference in age are *Mimomys primus*, present in the Hagerman fauna but absent in the Grand View, and species of *Ondatra*. *Ondatra* from Grand View may be slightly advanced over that from the older locality.

The rodent faunas of the Curtis and Benson are quite close to each other. A slight difference in age may be indicated in certain instances, in which cases the Benson fauna appears to be the older. The only extinct genus recorded from either assemblage is from the Benson. If a genus is represented in both faunas, the species are usually distinct, with some evidence that the Benson species are slightly less advanced. However, among rodents there does not seem to be the anomalous association of advanced and primitive types found among the larger mammals.

The Coso Mountains fauna is tentatively correlated with the Hagerman, since two of its types, a vole and a lagomorph, are probably identical with Hagerman species.

Only two rodent forms are known from the upper Etchegoin or San Joaquin clay. Deposition of the San Joaquin clay apparently represents a considerable period of time, and as the rodent types are separated stratigraphically as well as geographically, the "fauna" cannot be correlated exactly with any of the related upper Pliocene assemblages. One of the types occurring here, namely *Mimomys primus*, may be regarded tentatively as of the same age as the Coso Mountains and Hagerman faunas. The second rodent, *Castor californicus*, according to Stirton, is somewhat more primitive than the Hagerman beavers, and this fact suggests an age determination of the beds in which it occurs as slightly older than that of the Hagerman fauna.

It is quite possible that some of the faunas here referred to the upper Pliocene are actually lower Pleistocene. The possibility of this in connection with the San Pedro Valley assemblages has already been mentioned. The Grand View fauna may also be more appropriately placed in the Quaternary. Indeed, if views on the Pliocene-Pleistocene boundary expressed by several workers in the past ten years are applied to the faunas under discussion, most or all of them would be transferred to the Pleistocene.

Barbat and Galloway (1934, pp. 494-498) in a paper on the San Joaquin clay (upper Etchegoin) place the strata (zone "B" of these authors) in which *Mimomys primus* occurs in the lower Pleistocene. *Castor californicus* apparently is from their zone "C," which is designated lower Pleistocene, or transitional between the Pliocene and Pleistocene. They tentatively correlate zone "C" with the Cromer Forest Bed¹ and the Las Posas (first interglacial of California). Zone "B" was correlated with the Timm's Point of Southern California and the Mindelian glaciation of Europe. If Barbat and Galloway are correct in these tentative correlations, almost all of our upper Pliocene

¹ P. G. H. Boswell, in Proc. Geol. Assoc., 87-111, 1931, maintains that reference of the Weybourne Crag to a glacial stage or of the Cromer Forest Bed to a warm period is incorrect.

faunas could be placed in the lower Pleistocene. Even these authors leave the first glacial period (San Joaquin clay, zones "D" and "E"; Günz glaciation of Europe) in the upper Pliocene. According to the definition of the Pleistocene adopted by the United States Geological Survey, this stage should also be placed in the Quaternary. E. Haug has maintained this view in Europe, although most European palæontologists still include the first glaciation in the Pliocene.

The nearest equivalents in Europe of the Hagerman, Coso Mountains, and related faunas appear to be the Norwich Crag and Val d'Arno.¹ The latter are generally referred to the upper Pliocene, but also are usually considered as contemporaneous with the Günz glaciation. Thus according to American standards these faunas are of Pleistocene age, a view according to Matthew (1929, pp. 438-439) and Hay (1925, p. 240) that now finds other European supporters besides Haug.

One last point needs to be touched upon. It seems hardly likely that *Mimomys primus* occurs in a faunal stage which can be correlated with the Mindelian glaciation. *M. primus* is closest in characters to *M. pliocaenicus* of Europe. This latter species is typical of the Norwich Crag and extends no higher than the lower Cromerian. The genus *Mimomys* may extend into the Mindelian, but the various species in the European deposits are relatively short-lived. In view of the latter fact, it may be assumed, in absence of knowledge to the contrary, that the American species also had a limited range in time. Hence, since *M. primus* is somewhat more primitive than *M. pliocaenicus*, and this form in turn is in many ways the most primitive of known European representatives of the genus, it is improbable that the assignment of zone "B" to the Mindelian is correct unless a considerable homotaxial element enters into these relationships. However, I do not wish to imply that a genus of mammal or even an entire fauna is sufficient in the present state of our knowledge to permit intercontinental correlation involving such short periods of time as those represented by glacial and interglacial stages. Even the correlation of the North American upper Pliocene faunas with those of Europe that have been suggested in this paper may not be countenanced by many palæontologists. Correlation of a series of temperature changes for the Pleistocene on this continent with a similar series in Europe may be possible, with consequent establishment of rather exact time relations, but it should be mentioned that a solution of a similar problem presented by the Pleistocene of the British Isles and that of the European continent has not been reached with great success (Evans and Stubblefield, 1929, p. 498).

¹These European faunas do not appear comparable to our own "early Pleistocene" (i.e., Sheridan and equivalents), as W. D. Matthew believed.

Pliocene glaciation may account in part for the marked change in rodent faunas in the upper Pliocene, noted on previous pages. This change is sharper than any succeeding one, and from this standpoint the rodent assemblages now regarded as of the upper Pliocene might be more conveniently placed in the Pleistocene. In either case, it seems likely that some of the upper Pliocene rodent faunas discussed in the present paper belong to a period embraced by the first glacial and interglacial stages. This point is interesting since it has been maintained by some that the famous Rancho La Brea assemblage is Aftonian (first interglacial). As it is obvious that the faunas under discussion are in no way equivalent to Rancho La Brea, they furnish an additional reason for believing that the brea deposits are upper Pleistocene in age. This point has been mentioned before, but it bears repeating, since it applies not only to Rancho La Brea but to other deposits of similar faunal stage which have been referred to the lower Pleistocene.

Wherever the dividing line between Pliocene and Pleistocene may be drawn ultimately, the relative positions of the faunas are not altered. For this reason, and pending a fuller treatment of the subject by Mr. J. R. Schultz, the author prefers to keep the upper Pliocene rodent faunas where they are usually placed. The following chart (fig. 2) presents a tentative correlation of some Pliocene faunas based on a study of their rodent assemblages.

Pacific Coast Province		Great Basin Province	
		California	Arizona, Nevada, Oregon, Idaho
Upper	Upper Etchegoin <div>↕</div> { Mimomys Castor	Coso Mountains	Curtis Benson Grand View Hagerman
Middle	Kern River?		Rome Thousand Creek-Smiths Valley Rattlesnake
Lower	Siesta		 Fish Lake Valley

FIG. 2—Correlation chart showing time relationships of Pliocene rodent faunas

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CONTRIBUTIONS TO PALÆONTOLOGY

III

**A LATE CENOZOIC VERTEBRATE FAUNA FROM THE
COSO MOUNTAINS, INYO COUNTY, CALIFORNIA**

BY JOHN R. SCHULTZ

With eight plates and five text-figures

[Issued September 25, 1937]

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A LATE CENOZOIC VERTEBRATE FAUNA FROM THE COSO MOUNTAINS, INYO COUNTY, CALIFORNIA

INTRODUCTION

Isolated areas of sedimentary deposits flanking the eastern border of Owens Valley have attracted the attention of geologists since the period of the early surveys of this region. Discussion of the later geologic history of this part of the Great Basin, however, has been handicapped by lack of information concerning the age of the strata as determined by fossil evidence.

Walcott¹ listed fresh-water shells from beds exposed in Waucoba Canyon on the western flanks of the Inyo Range, and concluded that the sediments were lacustrine in origin and probably of Quaternary age. The present elevation of the beds above the valley was attributed to uplift subsequent to their accumulation.

Spurr² at a later time reviewed the literature then available and concluded that since similar deposits are found near the southern margin of Owens Valley, this basin formerly contained a lake approximately three thousand feet deep. In Spurr's opinion faulting had little to do with the present position of these beds. No additional fossil evidence was cited at the time.

More recently Knopf and Kirk³ demonstrated that the upper part of Walcott's "Waucobi" beds actually consists of alluvial materials which overlie unconformably the lake sediments, and that the faulting, to which the larger part of the present relief of the Inyo and Coso Ranges is due, must have occurred subsequent to deposition of the tuffs and alluvial deposits exposed on the western flanks of the Coso Mountains. Some poorly preserved ostracods were found in the tuff beds, but these furnished little evidence of value in making an age determination. While publication of this paper definitely establishes the occurrence of continental and lacustrine deposits of late Cenozoic age in a considerable portion of the area, recognition of the sequence of the later geologic events was based mainly on physiographic rather than on palæontological evidence.

More than six years ago fossil vertebrates were discovered in alluvial materials on the western flanks of the Coso Mountains. Since then the California Institute of Technology has conducted two collecting trips into the area: one during the winter of 1930-1931, the other dur-

¹ C. D. Walcott, *Jour. Geol.*, vol. 5, 340-348, 1897.

² J. E. Spurr, *U. S. Geol. Surv. Bull.* 208, 206-212, 1905.

³ Adolph Knopf and Edwin Kirk, *U. S. Geol. Surv. Prof. Paper* 110, 1918.

ing the summer of 1936. The collection now at hand consists of relatively few and fragmentary remains, but nevertheless fixes the age of these sediments within rather narrow limits on purely palæontological grounds. Some of the mammalian forms have already been described, but the present report aims to review the entire fauna and to include a brief account of the geologic relations of the fossiliferous beds.

Dr. Chester Stock placed the collection at the writer's disposal and furnished many helpful suggestions. I am further obligated to Dr. Stock for a critical reading of the manuscript. It is a pleasure to acknowledge the criticism of Dr. C. L. Gazin, whose knowledge of later Cenozoic vertebrate faunas has been helpful in clearing up doubtful points which appeared in the original text. The splendid cooperation in the field by R. M. Leard, G. A. Rynearson, and Jack Dougherty is gratefully acknowledged. In the course of the research many helpful suggestions have been made by R. W. Wilson, and E. L. Furlong has given advice and criticism. The illustrations are the work of John L. Ridgway.

GEOLOGICAL SETTING

Since the Coso Mountains occupy the northwestern corner of a geologically almost unexplored area extending from the Sierra Nevada on the west to Death Valley on the east, and from the Inyo Mountains on the north to the ranges bordering the Mojave Desert, some description of the geology seems desirable for a proper understanding of the significance of the fauna.

The central parts of the range consist of a very coarse-grained granitic rock. Lying upon its deeply weathered and eroded surface are a number of alluvial fans. These are best developed on the western flanks of the range and are well shown in Plate 1. Similar fans occur along the northern and northeastern borders of the mountains, but are either deeply dissected or covered by later deposits. South of the fossil quarries (see Plate 2) extensive beds of well-stratified tuff and volcanic breccia lie upon the granite. Both the alluvial and the tuffaceous materials dip away from the crest of the range at an angle varying from 6° to 10° . In places, however, the direction of dip is reversed, probably as a result of later folding and faulting. Near Haiwee reservoir Knopf and Kirk¹ describe the structure of the tuffs as anticlinal. In this region these authors have found fossil ostracods, which in the opinion of E. O. Ulrich are of Tertiary or later age, and indicate a marine connection with Owens Valley. Geologists prior to this find had considered these beds as lacustrine in origin. As Knopf and Kirk point out, a marine embayment in Owens Valley is so in-

¹ *Ibid.*, 51, 1918.

consistent with the better-known facts of the later geologic history of this part of California that it seems best to hold in abeyance the evidence of the ostracods until it is confirmed by additional data.

Lying above the tuffs is a basaltic lava from 50 to 100 feet thick. Wherever the contact is exposed, the lava is seen to be conformable with the underlying beds. In the Coso Mountains the lavas have been faulted at many points, while in the Inyo Range an extension of the flows has been displaced as much as 1400 feet by a series of step faults.¹ Following the faulting, deep canyons were eroded into the basalt and underlying beds, and Knopf and Kirk consider the physiographic features as evidence of an early Quaternary to late Pliocene age for the underlying sediments. Lavas of a later age occur in the region of Little Lake, approximately 25 miles south of the fossil locality, and it is probable that similar flows are to be found in the Coso Range, but the time available for the present study did not permit a sufficiently extended examination to establish this conclusion.

The relation of the alluvial material to the ostracod-bearing beds near Haiwee reservoir is of great importance, and it is unfortunate that it is not possible to determine definitely whether the coarse gravels in which the vertebrate fossils are found underlie the ostracod-bearing beds or, as Knopf and Kirk suggest, form a littoral phase of beds deposited farther out and in deeper water. However, the tuff bed overlying the vertebrate-bearing sediments is probably of the same age as that found near Haiwee reservoir where the ostracods were obtained. It thus appears that the subaqueous sediments are somewhat younger than the terrestrial deposits. Since fish remains are found only a few feet below the tuff in the region where the vertebrates were collected at locality 284, it seems reasonable to suppose that even at the time of accumulation of the terrestrial deposits the ancestral lake was in existence and not far away. The ostracod- and fish-bearing beds consequently may have accumulated during a later rise in water-level. It is tempting to regard this water body as an early stage in the history of Owens Lake, but definite proof that this was the case is difficult if not impossible to obtain.

Since the sedimentary deposits appear to form a unit and are sharply differentiated from all other rock types in the region, it seems appropriate to separate them as a distinct formation. The occurrence has already been mentioned in the literature as the Coso Mountains beds, and the name Coso formation is therefore applied to these deposits. Although the lavas are conformable with the Coso beds, it does not appear advisable to include them in the formation, for they are lithologically distinct and doubtless can be used as a separate mappable unit.

¹ *Ibid.*, 52, 1918.

In summary, the later geologic history of the Coso Mountains seems to fall into the following sequence: (1) faulting, or possibly warping, which elevated the granitic core and made possible the accumulation of alluvial fan material to a depth of at least 300 feet; (2) explosive volcanic activity giving rise to a considerable thickness of tuffaceous material, much of which appears to have been deposited in standing water; (3) extensive outflows of basaltic lava which covered the sedimentary materials and probably most of the granitic core as well; (4) faulting, probably entirely normal in displacement, followed by extensive erosion; and (5) in the area around Little Lake, and probably in the Coso Mountains as well, a second outpouring of basalt.

This history may seem excessively long and eventful to have taken place within Quaternary time. However, when compared with that of other areas, northern India particularly, where according to Colbert ¹ approximately 6000 feet of continental sediments were deposited since the beginning of the Pleistocene, it does not appear necessary to exclude any of these events from the Quaternary.

OCCURRENCE OF FAUNA

As mentioned on a preceding page, the vertebrate remains are found only in coarse alluvial fan deposits, which apparently underlie both the water-laid tuffs and the basaltic lavas. Although fossils were obtained from several rather widely separated areas (see Plate 2), the occurrence of what appears to be a continuous layer of tuff stratigraphically above the fossiliferous beds seems to justify the conclusion that the faunas are a unified assemblage from a single stage in geologic time.

Since the alluvial materials are of essentially the same character wherever found, a description of the principal fossil-bearing deposits will serve for all. As shown in Plate 2, these are located on the western flanks of the range almost due east and approximately 9.5 miles from the village of Olancho. Here the detrital materials consist of interstratified clay, coarse granitic debris, and rhyolitic tuff. The latter is confined to the upper portion of the section, where it forms a bed from 10 to 40 feet thick. A roughly estimated columnar section indicates the following sequence (reading from top to bottom): (1) the tuff bed mentioned above; (2) 100 feet or more of buff-colored arkose and clay with fossil localities 131 and 284 located near the base; (3) 30 to 40 feet of red shaly and arkosic material; (4) 50 feet of buff-colored clay and arkose; and (5) 40 feet or more of red beds and an unknown thickness of alluvial material below. It should be noted that the vertebrate remains were all obtained from a relatively narrow zone approximately 100 feet below the top of the tuff bed.

¹ E. H. Colbert, Trans. Amer. Philos. Soc., n.s., vol. 26, 9, 1935.

The total thickness of these deposits is difficult to determine since the base is exposed only at the upper end of the fan. If it is assumed that the more or less evenly graded side slopes of the canyon represent the original upper surface of the fan, 300 feet appears to be a minimum estimate. Such a determination means little, however, when it is recognized that the lower depositional surface is quite irregular, as demonstrated by the presence of granitic outliers entirely surrounded by fan material. A certain amount of overlap still further complicates the problem. The overlap is on no larger a scale than is to be expected in such deposits, however, and it seems probable that no significant time breaks exist in the section.

The vertebrate fossils appear to be confined to the coarse, arkosic beds in the upper half of the section. A total of nine quarries were opened, and practically all the material came from these excavations. Very little scattered material, occurring in outcrops, was sufficiently complete to be worth collecting. The quarried specimens are usually fragmentary and completely replaced by mineral matter. However, fairly well-preserved skulls and skeletal elements have been found. No articulated remains were recovered, suggesting that the skeletons were dismembered and washed down the slope prior to burial.

ENVIRONMENT OF FAUNA

There seems to be little doubt that the assemblage from the Coso beds was essentially one of the plains. This is indicated not only by the constituency of the fauna, but also by the relative abundance of certain types. For example, more than 40 per cent of the assemblage consists of horses of the genus *Plesippus*.

It seems reasonable to infer that the climate was somewhat more humid than that represented by the desert conditions now prevailing in the region. In view of the occurrence of water-laid tuffs either at the same stratigraphic level as the vertebrate horizon or slightly above, it may not be unduly speculative to infer that bodies of standing water were present and at no great distance from the fossil localities. The presence of *Mimomys* likewise suggests this conclusion, for at both the Hagerman, Idaho,¹ and Bakersfield, California,² localities where this vole has also been found, the geologic evidence points toward the presence of water bodies.

CORRELATION

The faunas more or less comparable to the Coso assemblage are listed below (pp. 84-86). For their locations see figure 1. There seems to be scant reason for considering any of these as very greatly

¹ C. L. Gazin, Proc. U. S. Nat. Mus., vol. 83, 285, 1936.

² C. J. Hesse, Jour. Mammalogy, vol. 15, 246, 1934.

different in age. Grand View, however, may represent a somewhat later stage; while a part of the San Pedro Valley beds (Benson locality), as well as the upper Etchegoin and part of the Blanco formation, may be somewhat older than the remaining faunas that have been listed.

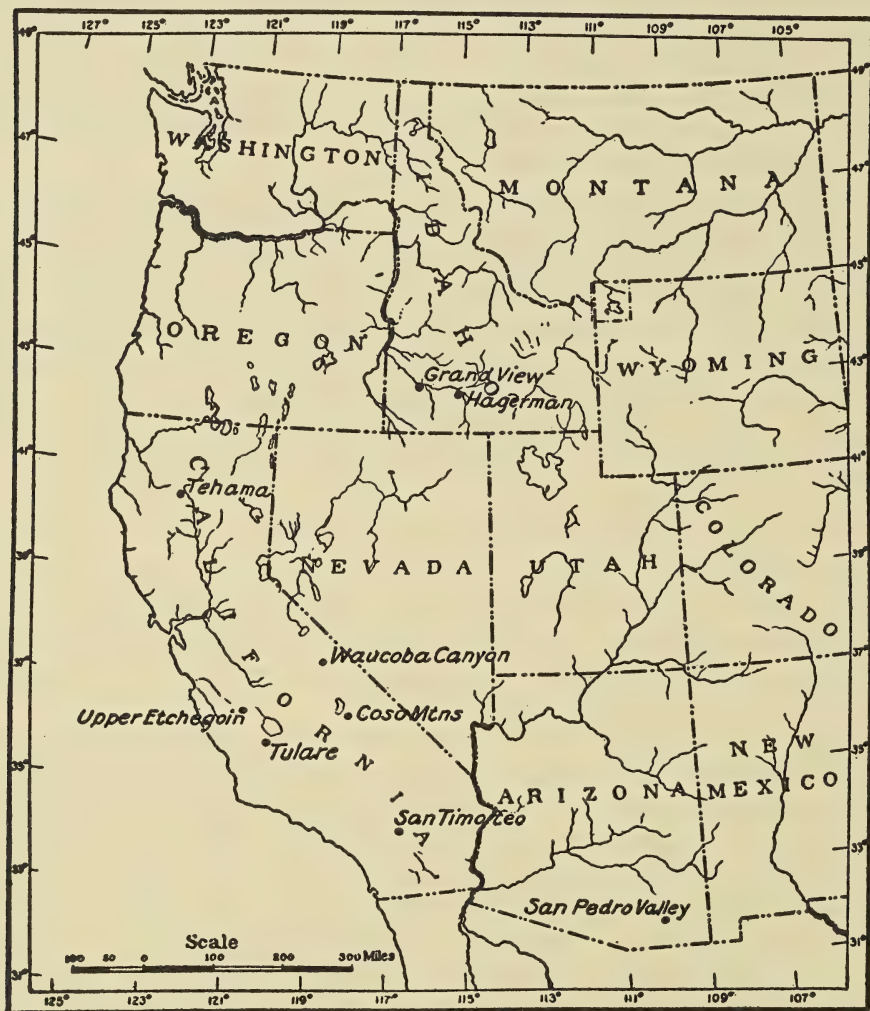


FIG. 1—Locations of the better-known upper Pliocene and lower Pleistocene vertebrate fossil localities in western United States.

While the evidence for these conclusions is incomplete, and especially so in the case of Grand View, the presence of such forms as *Anancus* and *Nannippus* may indicate that the Benson fauna is somewhat earlier than that from the Coso Mountains, which contains an advanced *Pliomastodon*? and a progressive species of *Plesippus*. The presence of *Osteoborus*? in the Blanco perhaps indicates an older

faunal stage near the base of that formation, or a late survival of this genus in the Texas region. Stirton and Vander Hoof¹ have suggested that this specimen along with *Plesippus cumminsii* comes from a zone below the Blanco. If this is true, the remainder of the fauna does not appear to be very much earlier in time than that of the Coso Mountains, for geographic separation may account for the remaining differences. Stirton² divides the upper Etchegoin into an upper or Buttonwillow assemblage and a San Joaquin fauna below. Since the latter is below the zone of *Mimomys primus*, it appears probable that the Buttonwillow fauna is more closely related in time to the Coso Mountains assemblage than is the San Joaquin fauna, which contains *Plesippus proversus* and *Pliomastodon vexillarius*—both more primitive types than the comparable *Plesippus francescana* and *Pliomastodon? cosoensis* from the Coso Range. It is not improbable that the Coso Mountains fauna is more closely related to the overlying Tulare than to any part of the upper Etchegoin. Proof of this supposition must await further discoveries of mammals in the Tulare.

Both Gazin³ and Wilson⁴ are of the opinion that the Grand View assemblage is slightly later in time than the Hagerman fauna. The age difference is not great, and seems to be based partly upon the apparently advanced characters of *Plesippus* (or *Equus*) *idahoensis* from Grand View in contrast to characters exhibited by *Plesippus shoshonensis* from Hagerman. If it is ultimately verified that the Hagerman assemblage is earlier in time than that of Grand View, there appears good reason for considering the age of the Coso assemblage as intermediate between these two Idaho occurrences, for while the horses from the California locality are, on the whole, more closely related to *Plesippus idahoensis* from Grand View, the remainder of the fauna is more like that from Hagerman.

Specimens of a fossil horse found in beds exposed in Waucoba Canyon, Inyo Mountains, are discussed in the present paper, since it seems probable that these beds are of essentially the same age as the Coso formation. The material represents parts of the axial and appendicular skeleton, but unfortunately does not include skull remains. A single metatarsal is shorter and somewhat more robust than is the average specimen of the corresponding element in *Plesippus francescana* from the Coso Mountains, but the metapodial appears to fall within the limits of variation of this element in *Plesippus francescana*. Furthermore, the splints show comparable reduction but are longer than in any species of *Equus* known to the writer. It is possible that

¹ R. A. Stirton and V. L. Vander Hoof, Univ. Calif. Pub., Bull. Dept. Geol. Sci., vol. 23, 176, 1933.

² R. A. Stirton, Amer. Jour. Sci., ser. 5, vol. 32, 180, 1936.

³ C. L. Gazin, *op. cit.*, 286, 1936.

⁴ R. W. Wilson, Carnegie Inst. Wash. Pub. No. 440, pt. 8, 121, 1934.

this metatarsal should be referred to *Plihippus*, but Dr. Stock recalls that fragments of an upper tooth (now lost) found in association with the limb material possessed an *Equus*-like protocone. The shortness of the metapodial recalls the genus *Hippidium*, but it does not appear probable that this South American form occurs at the Waucoba locality. Consequently, the material is tentatively referred to *Plesippus* or *Equus*.

Correlation of the Coso fauna with European assemblages rests mainly upon the vole, *Mimomys*, and to a lesser extent upon the horses of the genus *Plesippus*, which appear to be closely related to *Equus*? or *Plesippus? stenonis* of the Old World. As will be indicated on a later page, there is little doubt that in this instance an intercontinental correlation of reasonable accuracy is possible. The European equivalents are the Norwich Crag of England and at least the upper part of the Val d'Arno beds of Italy.

FAUNAS OF THE LATE PLIOCENE AND EARLY PLEISTOCENE

Coso Mountains

Borophagus solus (Stock)
Mimomys primus (Wilson)
Hypolagus near *limnetus* Gazin
Hypolagus small sp.
Platygonus sp.
Tanupolama? sp.
Plesippus francescana (Frick)
Pliomastodon? *cosoensis* n. sp.
 Fish remains

San Timoteo

Pliauchenia? sp.
Camelid small sp.
Cervid? medium n. sp.
Plesippus francescana (Frick)
Megalonyx? sp.

Hagerman

Borophagus sp.
Canid sp.
Lutravus? *idahoensis* Gazin
Lutravus? *cookii* Gazin
Lutra (*Satherium*) *piscinaria* Leidy
Felis lacustris Gazin
Machairodus? *hesperus* Gazin
Citellid sp.
Marmot sp.
Thomomys gidleyi Wilson
Castor accessor? Hay
Ondatra idahoensis minor Wilson
Mimomys primus (Wilson)

Tehama

Borophagus pachyodon (Merriam)
Canis near *ochropus* Eschscholtz
Prosthennops? or *Platygonus?* sp.
Camelops? or *Pliauchenia?* sp.
Antilocapra? sp.
Odocoileus? or *Cervus?* sp.
Plesippus proversus (Merriam)
Stegomastodon cf. *arizonæ* Gidley
Megalonychid gen. and sp.

Tulare

Borophagus pachyodon (Merriam)
Ischyrosmilus ischyurus Merriam

Elk Hills Tulare

Procamelus? sp.
Neotoma sp.
Sigmodon sp.
Lepus sp.

Grand View

Mimomys? *parvus* Wilson
Synaptomys vetus Wilson
Ondatra idahoensis idahoensis Wilson
Castor cf. *accessor* Hay
Erethizon bathygnathum Wilson
Lutra ingens Gazin
Hypolagus furlongi Gazin
Plesippus idahoensis (Merriam)

Waucoba Canyon

Plesippus? or *Equus?* sp.

Hypolagus near *vetus* (L. Kellogg)
Hypolagus limnetus Gazin
Alilepus? *vagus* Gazin
Platygonus n. sp.
Camelops? sp.
Procamelus? or *Tanupolama?*
Cervid sp.
Ceratomeryx prenticei Gazin
Plesippus shoshonensis Gidley
Mastodont sp.
Megalonyx leptonyx? (Marsh)
Blarina gidleyi Gazin
Pisces, *Amphibia*, *Reptilia*, and *Aves*

Blanco

Borophagus diversidens Cope
Amphicyon? sp. (probably *Borophagus*)
Canimartes cumminsii Cope
Osteoborus? *hillanus* (Cope)
Ænocyon cf. *dirus* (Leidy)
Platygonus bicalcaratus Cope
Platygonus texanus Gidley
Pliauchenia spatula Cope
Plesippus simplicidens (Cope)
Plesippus cumminsii (Cope)
Nannippus phlegon (Hay)
Neohipparion sp. (probably *Nannippus*)
Serridentinus præcursor (Cope)
Rhynchotherium falconeri Osborn
Cordillerion tropicus (Cope)
Stegomastodon successor (Cope)
Megalonyx leptostomus Cope
Mylodon sp. (probably *Megalonyx*)
Glyptotherium texanum Osborn

San Pedro Valley

Benson

Canid sp.
Mustelid sp.
Platygonus cf. *vetus*
Merycodus sp. (extremely doubtful)
Pliauchenia sp. *indet.*
Procamelus sp. *indet.*
Nannippus phlegon
Plesippus sp.
Anancus bensonensis Gidley
Citellus bensoni Gidley
Geomys minor Gidley

Curtis

Canid sp.
Mustelid sp.
Felid? n. sp.
Merycodus sp. (extremely doubtful)
Pliauchenia sp. *indet.*
Procamelus sp. *indet.*
Plesippus sp. (doubtful)
Equus sp.
Stegomastodon arizonæ Gidley
Lama n. sp.
Odocoileus n. sp.

Cratogeomys bensoni Gidley	Glyptotherium arizonæ Gidley
Dipodomys minor Gidley	Citellus cohesi Gidley
Cupidinus magnus (Kellogg)	Perognathus sp.
Peromyscus brachygnathus Gidley	Dipodomys minor Gidley
Peromyscus minimus Gidley	Dipodomys gidleyi Wood
Peromyscus sp.	Geomys persimilis Hay
Eligmodontia arizonæ Gidley	Onychomys pedroensis Gidley
Onychomys bensoni Gidley	Sigmodon curtisi Gidley
Sigmodon medius Gidley	Sigmodon minor Gidley
Neotoma fossilis Gidley	Neofiber sp.
Lepus sp. (very doubtful)	Lepus sp.
Sylvilagus or Brachylagus sp. (probably Hypolagus)	

DISCUSSION OF THE PLIOCENE-PLEISTOCENE BOUNDARY

Matthew ¹ pointed out that any attempt to correlate late Tertiary and early Quaternary deposits of North America with those of the European succession necessitates either a depression of the North American Cenozoic column, or an elevation of the European section. Such revision seems to be necessary by reason of the presence of *Equus* in the Pleistocene of North America and in the late Pliocene of the Old World. The writer ² attempted to remove this reason for shifting the boundary by referring the more primitive horses of the European species *Equus stenonis* to *Plesippus*, a genus which he considered to be characteristic of the late Pliocene of both the New and Old Worlds. In any event, the North American and European faunas of this stage are so similar as to leave little doubt concerning their approximate contemporaneity and the necessity of assigning them to the same period of geologic time.

It seems generally agreed that the late Pliocene of Europe, as represented by the Val d'Arno fauna of Italy, by various occurrences in the Puy de Dôme district of France, and by the Norwich Crag of England, marks the first appearance of the following genera: *Elephas*, *Bos*, *Equus* (possibly in part equivalent to *Plesippus*), and *Miomys*. Typical middle Pliocene genera which either become extinct or do not survive in the region are: *Hipparion*, *Viverra*, *Ailurus*, and *Semnophthecus*. The faunal turnover, although no more marked than that occurring between the lower and middle Pliocene, is nevertheless remarkable in that all of the new genera continue into the Pleistocene, and, with the possible exception of *Miomys*, all are immigrants.

Another important feature is the progressive lowering of temperature occurring at this time. This is indicated by the southward retreat of the macaques, and while it must be admitted that extinction of

¹ W. D. Matthew, Bull. Geol. Soc. Amer., vol. 35, 743-754, 1924.

² Carnegie Inst. Wash. Pub. No. 473, pt. 1, 12-13, 1936.

tropical forms is in evidence in northern Europe as early as the middle Pliocene, it is perhaps noteworthy that the upper Pliocene marks their final restriction to the Mediterranean region. Recent work by Boswell¹ indicates that by the time the Norwich Crag sediments were deposited, icebergs reached the English coast. While, as that author holds, this is scant evidence for correlating the Norwich Crag with the Günz glacial stage of the Continent, it is certainly prophetic of the Ice Age. Indeed, Reid Moir² is of the opinion that the Stone Bed beneath the Norwich and Weybourne Craggs was subjected to glaciation. This refrigeration is not evidenced by the terrestrial fauna alone, but by the marine invertebrates as well. The marine formations of England and Sicily show a sudden influx of northern species during this time, and while in the latter instance opening of the Straits of Gibraltar may have disturbed ecologic conditions, no such explanation is possible for the English locality.

It is not surprising that some European workers, notably Haug,³ on much the same evidence as that outlined above, have referred the Val d'Arno and Norwich Crag to the Pleistocene. To date Haug's views do not appear to have gained general acceptance in Europe, although Hay⁴ in North America endorsed this correlation.

If, as Forsyth Major⁵ has indicated, *Equus stenonis* of the Val d'Arno is closely related to *Equus sivalensis* from the upper Siwalik beds of India, there would appear to be good reason for considering both of these occurrences as lower Pleistocene in age. The evidence has been summarized by Colbert,⁶ who follows Matthew in holding that since these Eurasiatic forms seem to be derived from North American ancestors of the genus *Equus*, and as this genus is unknown in the latter continent before the advent of the Pleistocene, it follows that these Old World occurrences cannot be older than Pleistocene. It is interesting to note that Matthew⁷ apparently did not become convinced that the Val d'Arno should be referred to the Pleistocene until after he had studied the Siwalik problem in some detail. Even then he considered the Sheridan beds of Nebraska and the Val d'Arno as approximately equivalent. It seems more probable that the former are best correlated with Rancho La Brea and related occurrences, and that these are not of the same age as, but are younger than, the Val d'Arno and Norwich Crag. The equivalents of these Old World faunas apparently are the so-called upper Pliocene occurrences of western United States.

¹ P. G. H. Boswell, Proc. Geol. Assoc., vol. 42, 87-111, 1931.

² J. Reid Moir, Geol. Mag., vol. 69, 83-84, 1932.

³ Émile Haug, *Traité de Géologie*, 1767, 1922.

⁴ O. P. Hay, Jour. Wash. Acad. Sci., vol. 15, 239-241, 1925.

⁵ C. J. Forsyth Major, Quart. Jour. Geol. Soc. London, vol. 41, 3, 1885.

⁶ E. H. Colbert, Trans. Amer. Philos. Soc., n.s., vol. 26, 23-24, 1935.

⁷ W. D. Matthew, Bull. Geol. Soc. Amer., vol. 56, 438-443, 1929.

Genus	Middle Pliocene	Upper Pliocene	Pleistocene
1. Hypohippus.....		
2. Calippus.....	=====		
3. Pliohippus.....	=====		
4. Hipparion.....	=====		
5. Aphelops.....	=====		
6. Paraphelops.....	=====		
7. Teleoceras.....	=====		
8. Prosthennops.....	=====		
9. Alticamelus.....	=====		
10. Procamelus.....	=====
11. Pliauchenia.....	=====	
12. Sphenophalos.....	=====		
13. Ilingoceros.....	=====		
14. Merycodus.....	=====	
15. Blastomeryx.....		
16. Neotragoceras.....	=====		
17. Metoreodon.....		
18. Osteoborus.....	=====	
19. Ælurodon.....		
20. Tomarctus.....		
21. Aræocyon.....	=====		
22. Amphicyon.....	=====	
23. Brachypsalis.....	=====		
24. Sthenictus.....		
25. Agriotherium.....	=====		
26. Dinocyon.....	=====
27. Hyænarctos.....	=====		
28. Indarctos.....	=====		
29. Plionarctos.....	=====		
30. Machairodus.....	=====	
31. Adelphailurus.....	=====		
32. Pliogale.....	=====		
33. Plesiogulo.....	=====		
34. Mylagaulus.....	=====		
35. Eucastor.....	-----		
36. Dipoides.....	=====		
37. Liodontia.....	=====		
38. Diprionomys.....	=====		
39. Cupidininus.....	=====	
40. Pliosaccomys.....	=====		
41. Kansasimys.....	=====		
42. Pliozapus.....	=====		
43. Goniodontomys.....	=====		
44. Cernictis.....	=====		
45. Eomellivora.....	=====		
46. Nannippus.....	-----	=====	
47. Neohipparion.....	=====	=====
48. Lutravus.....	=====	=====	
49. Megatylopus.....	=====	=====	
50. Pliomastodon.....	=====	=====	
51. Anancus.....	=====	=====	
52. Ischyrosmilus.....	=====	=====	
53. Plesippus.....		=====	
54. Ceratomeryx.....		=====	
55. Borophagus.....		=====	
56. Felis.....	-----	=====
57. Platygonus.....	=====	=====
58. Camelops.....		=====	=====
59. Tanupolama.....		-----	=====
60. Ænocyon.....		-----	=====

FIG. 2 (continued on following page)

Genus	Middle Pliocene	Upper Pliocene	Pleistocene
61. <i>Lutra</i>		—————	—————
62. <i>Lepus</i>	—————
63. <i>Dipodomys</i>		—————	—————
64. <i>Onychomys</i>		—————	—————
65. <i>Sigmodon</i>		—————	—————
66. <i>Cratogeomys</i>		—————	—————
67. <i>Eligmodontia</i>		—————	—————
68. <i>Neotoma</i>		—————	—————
69. <i>Synaptomys</i>		—————	—————
70. <i>Mimomys</i>		—————	—————
71. <i>Ondatra</i>		—————	—————
72. <i>Erethizon</i>		—————	—————
73. <i>Mylohyus</i>		——— ———	—————
74. <i>Odocoileus</i>		——— ———	—————
75. <i>Canis</i>	——— ———	—————	—————
76. <i>Vulpes</i>	——— ———	——— ———	—————
77. <i>Ursus</i>	——— ———	——— ———	—————
78. <i>Pseudalurus</i>
79. <i>Taxidea</i>	—————	—————
80. <i>Mustela</i>	—————	—————	—————
81. <i>Martes</i>	—————	—————	—————
82. <i>Megalonyx</i>	——— ———	—————	—————
83. <i>Stegomastodon</i>	—————	—————	—————
84. <i>Hypolagus</i>	—————	—————	——— ———
85. <i>Sylvilagus</i>	——— ———	——— ———	—————
86. <i>Sciurus</i>	—————	—————	—————
87. <i>Castor</i>	——— ———	—————	—————
88. <i>Perognathus</i>	—————	—————	—————
89. <i>Thomomys</i>	—————	—————	—————
90. <i>Marmota</i>	—————	—————	—————
91. <i>Citellus</i>	—————	—————	—————
92. <i>Peromyscus</i>	—————	—————	—————
93. <i>Otospermophilus</i>	—————	—————	—————
94. <i>Geomys</i>	——— ———	—————	—————

————— Well-established range.

——— ——— Probable range.

. Reported, but probably not present in this range.

FIG. 2.—Ranges of some North American late Cenozoic mammalian genera.

Regardless of whether some of the European horses are to be referred to *Plesippus* rather than to *Equus*, since both these genera seem to have originated in the New World, it is of importance to determine the geologic epoch during which they appeared in North America. We are thus led to a consideration of the sequence on this continent.

Nearly all of the North American faunas of late Pliocene age, with the exception of the Peace Creek assemblage of Florida and the Loup River of Nebraska, have been plotted in figure 1 and listed on pages 84–86 of this paper. The two faunas mentioned above have been the occasion of so much misunderstanding that it seems best to exclude them from further consideration at this time. The faunas from

the Valley of Mexico present many anomalies, and are difficult to interpret. Freudenberg¹ distinguishes an upper Pliocene and a Pleistocene assemblage. More detailed field studies seem necessary before the validity of this division can be established. It seems best, therefore, to omit further reference in the present study to these interesting occurrences.

In another part of this publication Wilson² points out that between the middle and upper Pliocene appears a very important break in the character of the North American rodent faunas. The chart (fig. 2) has been prepared to show how this evidence parallels that of the larger mammals. The ranges of the various rodent genera follow Wilson's determinations. In preparing the chart the following faunas have been considered as middle Pliocene: upper Snake Creek, Rattlesnake, Thousand Creek, Kern River, and middle Etchegoin. The upper Pliocene is represented by the Blanco, Hagerman, Grand View, Tehama, upper Etchegoin, Tulare, Coso Mountains, San Pedro Valley, and San Timoteo assemblages. Location of these faunas is shown in figure 1. As is to be expected, many genera are doubtfully recorded, which gives rise to a serious problem of interpretation. Whenever an occurrence is considered as doubtful, but likely to be substantiated by the acquisition of more material, broken lines are used; the dotted segments indicate occurrences of a very doubtful and probably spurious nature.

In the discussion to follow the dotted portions will not be considered as a part of the range of a genus for the following reasons:

Procamelus? is listed from the upper Etchegoin,³ but since the determination is based on a fragmentary metapodial and is questioned by the original describer, the genus may be regarded as not extending its range above the middle Pliocene until further information demonstrates otherwise. The genus has been reported also from the Pleistocene of Arizona. Reasons for considering the generic reference of the material an error will be given on page 103 of this paper. There also appear to be good reasons for considering the material from San Pedro Valley, referred to this genus, as not belonging to *Procamelus*.

Merycodus is listed from the San Pedro Valley occurrence.⁴ A personal communication from C. L. Gazin states that the material probably does not represent that genus. Consequently, *Merycodus* is not regarded as ranging into the upper Pliocene.

Vander Hoof⁵ has shown that Cope's *Felis hillanus* from the Blanco is the genus *Osteoborus*. Since it has been suggested that the speci-

¹ Wilhelm Freudenberg, Geol. und Pal. Abhandl., neue Folge, Bd. 18, 104-105, 1922.

² R. W. Wilson, Carnegie Inst. Wash. Pub. No. 487, pt. 2, 58-63, 1937.

³ J. C. Merriam, Trans. Amer. Philos. Soc., n.s., vol. 22, 39, 1915.

⁴ J. W. Gidley, U. S. Geol. Surv. Prof. Paper 131, 120, 1922.

⁵ V. L. Vander Hoof, Cordilleran Section Geol. Soc. Amer., 35th Ann. Meeting, 32-33, 1936.

men, along with *Plesippus cumminsii*,¹ came from a faunal horizon below the Blanco, the evidence for the occurrence of *Osteoborus* in the upper Pliocene seems uncertain. *Plesippus* is here regarded as intermediate between *Pliohippus* and *Equus*, and even if it should be proved eventually that *Plesippus* occurs in the middle Pliocene, no significance from the standpoint of correlation can be attached to that fact.

Amphicyon? is listed as occurring in the Blanco.² Since the reference is everywhere questioned,³ and no description of the material is available, it seems best to regard the occurrence of the genus in the upper Pliocene as improbable.

Dinocyon? is reported from Hay Springs, Nebraska.⁴ The evidence consists of a metacarpal which may actually belong to a large ursid. Consequently, there appears to be little basis for extending the range of this genus beyond the middle Pliocene.

Machairodus? is reported from the Hagerman locality in Idaho.⁵ The material consists of a lower carnassial and a second metatarsal. Gazin remarks that the Idaho material seems very close to *Megantereon* from the Val d'Arno. While it is possible that the latter genus is synonymous with *Machairodus*, it does not appear advisable to consider the Hagerman material as conclusive evidence for an extension of the range of *Machairodus* above the middle Pliocene.

Pseudaelurus is recorded from the Pleistocene of Nebraska,⁶ but until the material upon which this reference is based is made known, it seems unwise to extend the range of the genus into the middle Pliocene, much less into the Pleistocene.

Cupidininus is reported from San Pedro Valley.⁷ The material consists of a part of an upper jaw with associated incisors. Since the latter are grooved, reference to *Cupidininus* is very doubtful. An extinct genus of rodent appears to be present at this locality, but an undescribed genus cannot be included in a chart of this kind.

Neohipparion is reported from the Aftonian of Iowa⁸ on evidence of a few teeth and limb elements. These certainly came from the glacial drift, but a little reflection upon the conditions under which such deposits are formed leads to the conclusion that the fragmentary remains may have been derived from Tertiary deposits. *Hipparion* is

¹R. A. Stirton and V. L. Vander Hoof, Univ. Calif. Pub., Bull. Dept. Geol. Sci., vol. 23, 176, 1933.

²H. F. Osborn, U. S. Geol. Surv. Bull. 361, 83, 1909.

J. C. Merriam, Univ. Calif. Pub., Bull. Dept. Geol., vol. 10, 434, 1917.

³C. L. Gazin, Proc. U. S. Nat. Mus., vol. 83, 288, 1936.

⁴W. D. Matthew, Bull. Amer. Mus., vol. 16, 317, 1902.

⁵C. L. Gazin, Jour. Mammalogy, vol. 14, 254-256, 1933.

⁶A. L. Lugen, Neb. Geol. Surv., Bull. 10, ser. 2, 212-213, 1935.

⁷A. E. Wood, Ann. Carnegie Mus., vol. 24, 146-148, 1935.

⁸O. P. Hay, Iowa Geol. Surv., vol. 23, 147-151, 1912.

listed from San Pedro Valley,¹ but Stirton² regards the occurrence as questionable. The latter author, however, lists both *Neohipparion* and *Nannippus* from this area. It is unfortunate that the evidence for these statements is not found in the literature. According to Gazin, the only horses found in the San Pedro Valley beds are *Nannippus*, *Plesippus*, and *Equus*.

Platygonus is reported from the Rattlesnake and middle Etchegoin beds. The material cited from the former locality is Marsh's *Platygonus rex*, which Thorpe³ regards as either *Prosthennops* or *Mylohyus* and more probably the former. It appears reasonable to regard the Rattlesnake specimen as a species of *Prosthennops*. The middle Etchegoin material consists of an astragalus of doubtful value in generic determination, and it is not at all certain that this specimen came from the upper rather than from the middle zone.⁴ Therefore, the uncertain identification of the material makes an extension of range of *Platygonus* prior to upper Pliocene a very doubtful procedure.

Prosthennops or *Platygonus* is listed from the Tehama.⁵ The material is an upper canine tooth. In the light of this inadequate evidence, sufficient reason does not appear available for recognition of range of *Prosthennops* above the middle Pliocene.

Tayassu or *Mylohyus* is reported from the upper Etchegoin.⁶ A more or less arbitrary disposition of this reference is made in the present paper. *Mylohyus* is regarded as extending into the upper Pliocene, while the range of *Tayassu* is considered as limited to the Pleistocene. This procedure is justified perhaps on the ground that neither has yet been reported from the middle Pliocene.

Odocoileus or *Cervus*⁷ is reported likewise from the upper Etchegoin, and a similar interpretation is made in this instance: *Odocoileus* is regarded as ranging down into the upper Pliocene, while *Cervus* is considered to be limited to the Pleistocene. It should be noted that although the alternative interpretation may prove eventually to be the correct one, in either case the statistical deductions, in a following paragraph, remain unaffected.

Although the segments that are dashed in the chart are considered as a part of the proved range of a genus, it is probable that future discovery will bring about considerable change in this portion of the graphic delineation. The solid lines indicate the unquestioned range of a genus according to present knowledge, but as taxonomy becomes more refined it is not improbable that some changes may occur also

¹ J. W. Gidley, *op. cit.*, 119, 1922.

² R. A. Stirton, Univ. Calif. Pub., Bull. Dept. Geol. Sci., vol. 23, 280, 1934.

³ M. R. Thorpe, Amer. Jour. Sci., ser. 5, vol. 7, 397, 1924.

⁴ J. C. Merriam, Trans. Amer. Philos. Soc., n.s., vol. 22, 32, 1915.

⁵ V. L. Vander Hoof, Amer. Jour. Sci., ser. 5, vol. 25, 384, 1933.

⁶ J. C. Merriam, *op. cit.*, 33, 1915.

⁷ *Ibid.*

in this part. In both cases, however, it is probable that approximately the same number of changes will occur in the columns for the middle Pliocene and Pleistocene. Such changes ought not, therefore, to affect materially the conclusions indicated below.

With the above reservations in mind, an examination of figure 2 discloses that out of the 94 genera considered, 87 have ranges sufficiently well known to be of value in the following discussion, and of these 39 apparently become extinct at the end of middle Pliocene time. This is essentially negative evidence, and it is not impossible that future work will demonstrate the presence of some of these genera in beds of later age. It does not appear probable, however, that the ranges now thought to end with the middle Pliocene will be extended upward to the same degree as will the ranges of upper Pliocene types into the Pleistocene. This is indicated by the fact that excluding the 19 long-range genera, 18 out of 28 which occur in the upper Pliocene begin there and extend into the Pleistocene, while of the remaining 10, 3 appear to be confined to the upper Pliocene. This leaves only 7 out of 28 upper Pliocene genera with a range from middle to upper Pliocene. In brief, the upper Pliocene fauna shows more affinity with the Pleistocene than with the middle Pliocene. The magnitude of the break between the middle and upper Pliocene is further emphasized when it is seen that among the families of larger mammals, the rhinoceroses and oreodonts apparently become extinct at the end of the middle Pliocene. This type of evidence can be easily overemphasized, however, for some of the larger mammals may have died out even before that time. In the case of the rodents, as Wilson¹ has indicated, the predominant forms of the middle Pliocene and earlier stages are sciurormorphs, whereas with the beginning of the upper Pliocene the myomorph group becomes important for the first time. It is also interesting to note that the upper Pliocene marks the first undoubted appearance of hystricomorphs on this continent. The only rodent family which apparently becomes extinct at the end of the middle Pliocene is the Mylagaulidæ. In the light of the statements made above, this extinction may assume considerable importance. Indeed, the evidence from the mammalian fauna is so striking that on this basis alone, there appears to be good reason for extending the Pleistocene boundary to the base of the so-called upper Pliocene. That the period of time involved in this shift is not long, and therefore does not reduce the length of the Pliocene unduly, is indicated perhaps by the fact that only three genera, *Ceratomeryx*, *Plesippus*, and *Borophagus*, seem to be limited to the upper Pliocene, and one of these (*Plesippus*) as here defined is essentially transitional between the middle Pliocene *Pliohippus* and Pleistocene *Equus*. While definition

¹R. W. Wilson, Carnegie Inst. Wash. Pub. No. 473, pt. 2, 18, 1936.

of the Quaternary is in no sense dependent upon a faunal break of this kind, from the viewpoint of the vertebrate palæontologist it would seem desirable to consider this break in the succession of mammalian forms as marking the Pleistocene-Pliocene boundary.

Since the Pleistocene is usually thought of as the glacial period, it is important to see if the evidence does not suggest an important climatic change during the upper Pliocene. Dorf¹ has shown that the upper Pliocene floras of California indicate a more humid climate than middle Pliocene assemblages from the same area, and this author considers the increasing humidity to be indicative of a general lowering of temperature leading directly into the glacial period. However, as Dorf himself indicates, the climate of Santa Clara Valley in middle California may have been more humid during the upper Pliocene simply because the Coast Range barrier, which now prevents the passage of moisture-laden clouds over the area, was not in existence at that time. But, as this author points out, such topographic conditions should lead to a raising rather than to a lowering of temperature, and since the Santa Clara flora is of a montane aspect, the evidence, although not overwhelming, rather tends to point toward a widespread lowering of temperature during that time.

The mammalian faunas offer no conclusive climatic evidence, but the sudden appearance of voles, as for example *Mimomys*, is at least suggestive, for these creatures find their most congenial habitat in boreal regions. It is perhaps not unduly speculative to assume that the peculiar faunal mixtures of San Pedro Valley and the Valley of Mexico reflect a migration of northern forms into these areas in response to a general lowering of temperature. Interestingly enough, Gidley² actually suggested migration as an explanation for the differences between the Benson and Curtis localities, but did not correlate this with any significant climatic change. The view takes on some plausibility when it is recalled that all of these "mixed" faunas are found in southern latitudes: Arizona, the Valley of Mexico, and Miñaca³ in northern Mexico. When traced northward, faunas of approximately the same age, as for example those along the Snake River in Idaho, show no evidence of mixing.

In a recent paper Barbat and Galloway⁴ present the view that the upper part of the upper Etchegoin, or San Joaquin Clay in the nomenclature of these authors, is characterized in certain zones by marine invertebrates of a cold-water habitat. Although these authors correlate the San Joaquin Clay with the Norwich Crag and related Euro-

¹ Erling Dorf, Carnegie Inst. Wash. Pub. No. 412, pt. 1, 55, 1933.

² J. W. Gidley, U. S. Geol. Surv. Prof. Paper 140, 84, 1926.

³ Study of the fauna from Miñaca is now in progress.

⁴ W. F. Barbat and J. Galloway, Bull. Amer. Assoc. Pet. Geol., vol. 18, 491, 498, 1934.

pean occurrences, they regard all as of upper Pliocene age. Bailey¹ and Cross² have shown that the Santa Barbara formation of southern California may be more properly referred to the Pleistocene than to the Pliocene, since evidence of cooler water during its deposition is not wanting. However, climatic inferences drawn from fossil invertebrate faunas frequently need to be tempered by proper evaluation of factors which tend to influence these assemblages, as, for example, the bathymetric range of organisms and the configuration of the coastline at particular periods of time.

In summary it may be said that the upper Pliocene of North America, on the evidence of the flora as well as on that of the terrestrial faunas, seems to be marked by a cooling climate which may have led directly into glacial conditions. However, substantial support of this view still needs to be furnished by the fossil invertebrate faunas.

At least some of the so-called upper Pliocene vertebrate assemblages of western United States could be referred to the Pleistocene without much hesitation were it not for the aspect of the Aftonian fauna of Iowa.³ A definite placement of this assemblage in deposits formed during the first interglacial epoch would tend to emphasize the faunal disparity between it and the western, so-called upper Pliocene faunas of the preceding glacial epoch because of the shortness of the intervening period. A study of the fauna from McKittrick, California, now in progress, convinces the writer that this assemblage and that of Rancho La Brea (typically Aftonian according to Hay) are actually late Pleistocene in age. Most significant of all, recent work by Kay and Apfel⁴ has demonstrated that it is impossible for glaciologists to determine with any degree of accuracy the position of the beds in which the "Aftonian" fauna was found. The deposits are either Kansan or Nebraskan in age, and not Aftonian. It must be admitted that these authors incline toward the view that the "Aftonian" fauna is Nebraskan, but no convincing evidence as to why it could not be referred to the succeeding Kansan glacial epoch is offered. If, as the writer is inclined to believe, the "Aftonian" fauna is actually Kansan or perhaps even Yarmouth, it is not improbable that the "upper Pliocene" faunas of the western states are at least in part referable to the first glacial epoch. As has been indicated, the period of time represented by these faunas does not appear to be long, and it is interesting to note that glaciologists consider the Aftonian as one of the longest of the interglacial epochs.⁵

¹ T. L. Bailey, *Bull. Geol. Soc. Amer.*, vol. 46, 494, 1935.

² R. K. Cross, *Cordilleran Section Geol. Soc. Amer.*, 35th Ann. Meeting, 5, 1936.

³ O. P. Hay, *Iowa Geol. Surv.*, vol. 23, 147-151, 1912.

⁴ G. F. Kay and E. T. Apfel, *Iowa Geol. Surv.*, vol. 34, 193-195, 209-211, 1929.

⁵ G. F. Kay, *Bull. Geol. Soc. Amer.*, vol. 42, 464, 1931.

The Nebraska Geological Survey¹ has as yet discovered no vertebrate fauna in the earliest glacial drift, and the definitely recorded Aftonian and Kansan occurrences in that state are few. Pertinent to the present discussion is the fact that geologists of the Nebraska survey² now consider the Sheridan beds (also Aftonian in Hay's classification) as probably middle Pleistocene in age. The conclusion seems inescapable that early Pleistocene vertebrate faunas are as yet practically unknown in the Great Plains region, and that elevation to that position in time of at least some of the upper Pliocene assemblages of the western states fills the gap now in the record. It should be indicated again, however, that the lower parts of the upper Etchegoin and Blanco formations, as well as the Benson locality, may be pre-Nebraskan in age. Reasons for considering even these as Pleistocene will be given in a following paragraph.

In view of Romer's excellent summary of the Pleistocene,³ it is unnecessary to discuss the Aftonian problem further, other than to point out that although Hay's methods appeared sound, they have never led, and probably never will lead, to satisfactory results. Even if the fauna is proved to come from Aftonian deposits, distant correlations with it must remain a difficult task. The reasons are not far to seek, and have been pointed out by Simpson⁴ and others. The fallacy appears to lie in a neglect to bring together all possible lines of evidence. This appears to be particularly unfortunate when dealing with a period as varied in its physical history as is the Pleistocene. In the last analysis, the only possible definition of this period must be essentially climatic. For this we have no less an authority than Suess,⁵ who said: "But it is scarcely necessary to remark that, while characters of the terrestrial fauna afford a most valuable passive criterion, yet it is the physical causes of faunal transformations which will, when once they are recognized, form the only true basis for a delimitation of chronological periods."

In the writer's opinion the most widespread physical event separating the Pliocene and Pleistocene is change in climate. Consequently, where such a change is indicated by data derived from the faunas, floras, or sedimentary record, the boundary should be established even if some of this evidence is ultimately shown to be based on deposits that antedate the earliest known glacial drift. In no other way can the anomalous recognition of glacial stages in the Pliocene, as has been maintained in Europe, be avoided. Isolated and distant occurrences will perhaps never be satisfactorily correlated with those of the drift

¹ A. L. Lugen and C. B. Schultz, *Neb. State Mus. Bull.* 41, vol. 1, 358, 1934.

² A. L. Lugen, *Neb. Geol. Surv., Bull.* 10, ser. 2, 192, 1935.

³ A. S. Romer, *The American Aborigines*, 49-83, Toronto, 1933.

⁴ G. G. Simpson, *Bull. Amer. Mus.*, vol. 59, 173-175, 1930; *Amer. Mus. Novitates*, No. 667, 7, 1933.

⁵ E. Suess, *Face of the Earth*, Eng. trans., 14, 1904.

areas. Moreover, no formidable reason appears to exist why glaciologists should object to a downward extension of the Pleistocene. Indeed, it is perhaps pertinent to suggest that much of the difficulty of the past has come about as a result of too much preoccupation with glacial phenomena, for the "glacial drift" itself is nothing more than evidence of marked climatic change. It is reasonable to assume that the effects of lowering temperature made themselves felt in the terrestrial fauna considerably before the time when recognizable traces were left by an advancing ice sheet. Matthew¹ in his later years apparently tended to favor this view.

To summarize, elevation of the European and North American upper Pliocene faunal stages to the Pleistocene would, in the light of present knowledge, involve the following improvements in stratigraphic and palæontological usage: (1) it places the boundary at the lowest, and perhaps most significant, faunal and climatic break separating the late Tertiary and early Quaternary; (2) it furnishes a lower Pleistocene vertebrate fauna heretofore very imperfectly known; and (3) it permits a fairly close correlation of European and North American vertebrate faunas without necessity of either elevating the European or depressing the North American column.

To change a generally accepted view requires well-nigh overwhelming evidence, and it must be admitted that in the present instance such change is advocated only if it represents the conclusion derived from a workable hypothesis. Therefore, the writer neither expects nor wishes immediate acceptance of this view. Further exploration coupled with exact field work and careful collecting in the Snake River region of Idaho, the Valley of Mexico, and in the Paso Robles and Tulare beds of California may throw much needed light on the problem. In addition, a restudy of European faunas by an investigator familiar with the late Pliocene and early Quaternary assemblages of the western United States may yield much profitable information.

Objections which may be offered to the above conclusions are: (1) The faunal break between the middle and upper Pliocene is not so abrupt as it appears to be from figure 2. Old forms probably died out at various stages of the middle Pliocene, while new genera probably appeared at various stages of the upper Pliocene. (2) Migration from Eurasia and South America was under way even before the upper Pliocene, as is evidenced by the occurrence of the Asiatic genus *Eomellivora* in the Kern River deposits and by the presence of ground-sloths in the Rattlesnake. (3) The climatic evidence, especially in the case of the invertebrates, is not conclusive. (4) As yet the terrestrial faunas of the western states have not been tied in with either the marine section or the glacial drift.

¹ W. D. Matthew, Bull. Amer. Mus., vol. 56, 439, 1929.

In view of the present imperfect state of knowledge concerning the succession in western United States, the following tentative correlation is proposed. Since both invertebrate and vertebrate palæontologists seem generally agreed that the upper Etchegoin belongs in the upper Pliocene, it is placed with the Benson beds in the very latest Pliocene. Grand View, Curtis, and at least the upper part of the Tulare appear to be of lowest Pleistocene age; while the Blanco, Hagerman, Tehama, San Timoteo, Coso Mountains, and perhaps the lower part of the Tulare as well, may, for want of a more suitable assignment, be regarded as transitional. These conclusions are summarized in figure 3.

	EUROPE		NORTH AMERICA
Lower Pleistocene	Upper Val d'Arno	} Zone of <i>Mimomys</i>	Curtis, Grand View, Tulare
Transitional	Cromerian Weybournian Chillesfordian		San Timoteo, Blanco, Hagerman, Coso Mountains, Tehama
Upper Pliocene	Norwich Crag		Upper Etchegoin (including San Joaquin Clay) Benson

FIG. 3—Tentative correlation of upper Pliocene and lower Pleistocene of Europe and western North America.

SYSTEMATIC DESCRIPTION OF FAUNA

Borophagus solus (Stock)¹

A palate, No. 481, Calif. Inst. Vert. Pale. Loc. 131, with an upper dentition serves as the type of this species. The original reference was to *Hyæognathus*, but since the description was published Vander Hoof² has succeeded in recovering the lost type of Cope's genus, *Borophagus*, and is of the opinion that *B. diversidens* and *H. pachyodon* are identical. No further information is available to the writer, and since Vander Hoof's statement is the latest reference to the question, it seems advisable to follow that author. The only new material available from the Coso Mountains is a fragment of palate, No. 2024, from locality 284, containing the heel of M₁ and the roots of P₄. Unfortunately, this specimen adds nothing to our knowledge of the species, but is referable without question to *B. solus*.

A fragmentary ulna, No. 2025, C.I.T. Loc. 131, is somewhat larger than the comparable element of *B. cynoides*,³ but since the skull of *B. solus* is

¹ Chester Stock, Jour. Mammalogy, vol. 13, 263-266, 1932.

² V. L. Vander Hoof, Cordilleran Section Geol. Soc. Amer., 35th Ann. Meeting, 32-33, 1936.

³ W. D. Matthew and R. A. Stirton, Univ. Calif. Pub., Bull. Dept. Geol. Sci., vol. 19, pl. 32, 1930.

correspondingly larger than that of *B. cynoides*, one may reasonably infer that the ulna from the Coso Mountains belongs to Stock's species.

Plesippus francescana (Frick)

Horse material from Calif. Inst. Vert. Pale. Loc. 131, consisting of fragmentary palates, lower jaws, and various limb elements, was referred by the writer¹ to *Plesippus francescana*, a species originally described by Frick from the San Timoteo beds of southern California. At the same time reasons for referring the species to *Plesippus* were given. All the dentitions then available were in an advanced stage of wear, but since they approximated the type in this respect as well, the reference seemed justified. However, for purposes of correlation, too much reliance cannot be placed upon minor characters of equine teeth. In the present instance, the rather primitive features of the enamel pattern of *P. francescana* appeared somewhat anomalous, for the Coso fauna as a whole gave evidence of a more advanced character than that furnished only by the horses. Fuller collections have been brought together and the opportunity is taken, therefore, to supplement the information regarding *P. francescana*. It can now be said that, judging from relatively unworn dentitions, Frick's species seems to be an advanced rather than a primitive *Plesippus* type.

The skull from locality 284, No. 2020 (Plate 3), is crushed, but is the only cranial specimen available of this species. The specimen belongs apparently to a young adult, for while the dentition is rather well worn, the sutures are not entirely closed.

Skull Characters—The specimen is too crushed to give reliable estimates of cephalic indices. However, in size *P. francescana* probably compares favorably with *P. shoshonensis*. Although the backward curvature of the occiput seems to be slightly less than that in the Hagerman species, the occipital crest is directed nearly straight backward. The middle portion of this crest is notched as in *P. shoshonensis*. Little evidence of this notch is present in *Equus occidentalis* from Rancho La Brea. The fronto-nasal suture forms a sharp, forwardly directed V on the median line of the skull. In this character the Coso Mountains form is quite similar to *P. shoshonensis*, but differs from *E. occidentalis* from McKittrick, California. In the latter the forward portion of this suture often outlines a broadly open U rather than a sharp V. As in the Hagerman species, a long and deep fossa lies above and posterior to the infraorbital foramen. This depression is practically wanting in *E. occidentalis*. The external auditory meatus is directed backward and upward, much as in *P. shoshonensis*. The posterior palatine foramina, as in the latter species, are located opposite M₂; the anterior margin of the posterior nares is located in line with the boundary between the second and third upper molars, rather than in line with the middle of M₂ as in the Idaho material.

In summary, it may be stated that while the skull of *P. francescana* resembles that of *P. shoshonensis*, it differs from the latter in the following particulars: (1) slightly less backward projection of the occiput, and (2) more posterior position of the posterior nares.

Points of major difference between *P. francescana* and *E. occidentalis* are: (1) absence of a re-entrant V-shaped incision on the occipital crest; (2) presence of a V-shaped median portion of the fronto-nasal suture; and (3) presence of a well-marked nasal-lachrymal fossa. The position of the

¹ Carnegie Inst. Wash. Pub. No. 473, pt. 1, 1-13, 1936.

posterior nares in *E. occidentalis* is very similar to that seen in *P. shoshonensis*.

Dentition—As shown in figure 4, the dentition of specimen No. 2020, Loc. 284, although only slightly more worn than that of No. 2016, Loc. 131, nevertheless differs markedly from the latter in much shorter antero-posterior diameter of the protocone and in the absence of any well-marked indentation of the inner walls of this cusp. It is also worthy of note that specimen 2020 in contrast to No. 2016 shows no well-marked pli caballin in any teeth except P₂ and M₁. Indeed, in characters of the

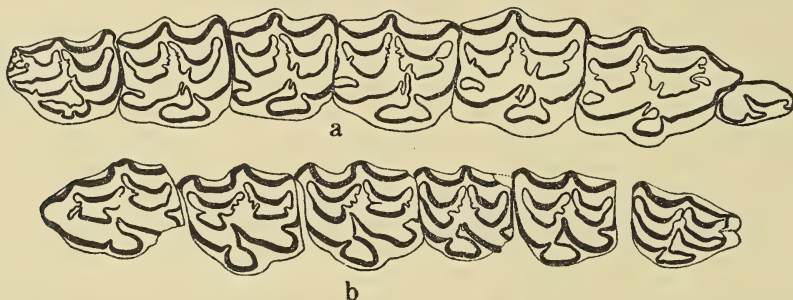


FIG. 4—*Plesippus francescana* (Frick). a, No. 2016, Calif. Inst. Loc. 131, $\times \frac{1}{2}$; b, No. 2020, Calif. Inst. Loc. 284, right side (reversed in printing), $\times \frac{1}{2}$.

enamel pattern the former approximates *P. proversus*, while the latter is allied to *P. idahoensis*. However, since the two specimens agree closely in measurements of teeth (see table), especially P₃ to M₂ inclusive in comparable stages of wear, and since they fall within the range of individual variation given by Gidley, it appears reasonable to conclude that *P. francescana* exhibits an enamel pattern varying from a type almost indistinguishable from that of *P. proversus* to one closely approximating that of *P. idahoensis*. This conclusion seems justified, furthermore, by the consideration that measurements of the teeth of *P. francescana* differ by 3 to 5 millimeters from those of *P. proversus*¹ and *P. idahoensis*.²

The additional lower dentition now available, No. 2021, Loc. 131, differs somewhat from specimen No. 902. As shown by Plate 4, figure A, the gutter marking the separation of the metaconid from the metastylid is much more broadly open, especially in the premolars, and the metaconid-metastylid column somewhat flatter than in No. 902.³ In both characters specimen No. 2021 closely parallels *P. idahoensis*, but here again the difference in tooth dimensions indicates that the form cannot belong to the Idaho species.

*Measurements (in millimeters) of Permanent Dentition of Plesippus francescana (Frick)*⁴

	No. 2016	No. 2020
Length of upper molar-premolar series with P ₁	196.0
Length of upper premolar series without P ₁	101.4	99.0
Length of upper molar series.....	82.0	75.5
P ₂ , antero-posterior diameter.....	39.0	37.0
P ₂ , transverse diameter.....	27.3	26.8
P ₃ , antero-posterior diameter.....	31.3	29.6
P ₃ , transverse diameter.....	28.8	27.3

¹ J. C. Merriam, Univ. Calif. Pub., Bull. Dept. Geol., vol. 9, 534, 1916.

² J. C. Merriam, Univ. Calif. Pub., Bull. Dept. Geol., vol. 10, 530, 1918.

³ For illustration of this specimen see Carnegie Inst. Wash. Pub. No. 473, pt. 1, 6, fig. 2a, 1936.

⁴ For explanation of system of measurements see J. C. Merriam, Univ. Calif. Pub., Bull. Dept. Geol., vol. 7, 409, 1913.

Measurements (in millimeters) of Permanent Dentition of Plesippus francescana (Frick)
(Continued)

	No. 2016	No. 2020
P ₄ , antero-posterior diameter.....	29.8	29.0
P ₄ , transverse diameter.....	27.5	27.5
M ₁ , antero-posterior diameter.....	25.3	24.0
M ₁ , transverse diameter.....	25.7	25.8
M ₂ , antero-posterior diameter.....	26.8	25.5
M ₂ , transverse diameter.....	25.8	24.0
M ₃ , antero-posterior diameter.....	28.0	25.5
M ₃ , transverse diameter.....	21.0	19.0
		No. 2021
Length of lower molar series.....		90.0
Length of lower premolar series.....		95.0
P ₂ , antero-posterior diameter.....		34.5
P ₂ , transverse diameter.....		15.8
P ₃ , antero-posterior diameter.....		30.5
P ₃ , transverse diameter.....		17.4
P ₄ , antero-posterior diameter.....		30.0
P ₄ , transverse diameter.....		16.5
M ₁ , antero-posterior diameter.....		26.4
M ₁ , transverse diameter.....		12.5
M ₂ , antero-posterior diameter.....		28.0
M ₂ , transverse diameter.....		15.5
M ₃ , antero-posterior diameter.....		35.0
M ₃ , transverse diameter.....		12.0
I ₂ , greatest transverse diameter.....		12.8
I ₂ , greatest transverse diameter.....		15.0
I ₃ , greatest transverse diameter.....		16.0
C, greatest antero-posterior diameter.....		15.0

Platygonus sp.

Referred material—The anterior portion of a lower jaw, No. 1850 (Plate 8, fig. 6); two well-worn first lower? molars, Nos. 1850a, b (Plate 8, figs. 4, 5); and a third lower molar, No. 1850c (Plate 8, fig. 3). All from Calif. Inst. Vert. Pale. Loc. 131.

Description—The symphyseal region has been crushed in No. 1850 so as to cause the incisors to be directed almost straight forward. I₁ is nearly square in outline. It thus differs from I₂, which is larger, and rounded in cross-section. I₃ is a peg-like tooth of elliptical outline, the longer axis of the ellipse being directed antero-posteriorly. The canines are scimitar-like tusks, and curve out and a trifle backward.

The crown of M₁? is too worn to show much, but two transverse crests were evidently present. Each crest was probably divided into two cusps by a longitudinal furrow. The valley between the transverse crests is obstructed by a very small longitudinal projection from each of the two main crests. A rather short transverse cingulum is present on both the anterior and posterior margins of the tooth.

M₃ is practically unworn. The crown pattern consists of two subequal transverse crests with a large heel. Each crest is divided into two sharp cusps by a V-shaped longitudinal cleft. The intervening transverse valley is interrupted by a longitudinal extension of the transverse crests similar to, but larger than, that seen in M₁?. The heel consists of one large cusp with a much smaller cuspule on either side. The valley separating the heel from the second transverse crest is interrupted also by a forward extension of the heel. Slight traces of a cingulum occur along the anterior margin of the tooth.

Comparisons—This specimen resembles in some respects *Mylohyus* and *Tayassu*, as well as *Platygonus*. Reference to *Mylohyus* seems excluded, however, since this genus is characterized by only two lower incisors.¹ *Tayassu* likewise seems excluded by virtue of the low, blunt-conical tubercles which characterize that genus.

¹ Barnum Brown, Mem. Amer. Mus., vol. 9, 201, 1908.

The specimen from the Coso Mountains appears to show some resemblance to material from the McKittrick asphalt described by Stock¹ as *Platygonus* near *compressus* LeConte. Points of major difference are the somewhat larger size and better-developed transverse cingulum seen in the McKittrick specimen.

Considerable difference apparently exists between the Coso Mountains material and a third lower molar described by Merriam² from the upper Etchegoin, and referred to either *Tayassu* or *Mylohyus*. The chief differences are the absence of the deep V-shaped longitudinal clefts separating the main cusps, and the lower and more blunted tubercles seen in the Etchegoin specimen.

Measurements (in millimeters) of Platygonus sp.

	No. 1850
II, greatest longitudinal diameter.....	5.0
II, greatest transverse diameter.....	5.7
I2, greatest longitudinal diameter.....	6.0
I2, greatest transverse diameter.....	6.5
I3, greatest longitudinal diameter.....	4.6
I3, greatest transverse diameter.....	5.2
C, greatest antero-posterior diameter.....	18.8
C, greatest transverse diameter.....	12.0
	No. 1850a
MI?, greatest antero-posterior diameter.....	14.0
MI?, greatest transverse diameter.....	10.0
	No. 1850c
M3, greatest antero-posterior diameter.....	25.0
M3, greatest transverse diameter.....	13.3

Tanupolama? sp.

Referred material—A first and a second lower molar, Nos. 2022 (figs. 5a, c); and a first phalanx, No. 2023 (fig. 5b). The teeth are from locality 131; the phalanx from locality 284.

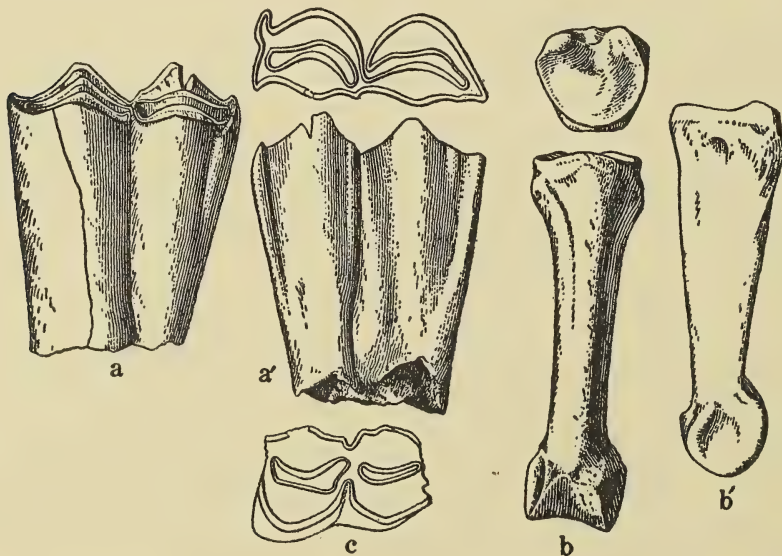


FIG. 5—*Tanupolama? sp.* a, M2, No. 2022, Calif. Inst. Loc. 131, $\times 1$; b, phalanx I, No. 2023, Calif. Inst. Loc. 284, $\times \frac{1}{2}$; c, MI, No. 2022, Calif. Inst. Loc. 131, $\times 1$.

¹ Chester Stock, Carnegie Inst. Wash. Pub. No. 393, pt. 3, 25–27, 1928.

² J. C. Merriam, Trans. Amer. Philos. Soc., n.s., vol. 22, 36–37, 1915.

Comparisons—The teeth are somewhat narrower transversely than corresponding elements of *Tanupolama stevensi* from McKittrick, California.¹ This may be due to stage of wear, since the material from the Coso Mountains is less worn than any of the McKittrick specimens available for comparison. In all other details, and especially in the presence of an antero-internal as well as an antero-external style on M2, the specimens in question closely approximate the type. The first phalanx is proportionately a trifle more slender than the average of corresponding elements of *T. stevensi*, but individuals of nearly the same size and proportions as No. 2023 can be selected from the McKittrick material. While the material from the Coso Mountains is too incomplete to permit conclusive generic determination, the close agreement with *Tanupolama* in both tooth and limb characters seems to indicate a form not far removed from that genus.

While it must be admitted that phalanx No. 2023 is quite similar to that of *Procamelus longurio* Hay² from the Pleistocene of Anita, Arizona, it is not entirely clear that the Arizona material is to be referred to *Procamelus*. Indeed, there seems to be little reason why Hay's species should not be referred to *Tanupolama*. In the past it seems to have been the almost general practice to refer all slender-limbed camels to either *Procamelus* or *Pliauchenia*, and little is to be gained from further discussion until the later Tertiary camels have been thoroughly revised. It should be noted, nevertheless, that Stock's recognition of the genus *Tanupolama* makes this procedure very questionable when dealing with forms of late Tertiary and Quaternary age.

Measurements (in millimeters) of Tanupolama? sp.

	No. 2022
MI, antero-posterior diameter.....	22 (a)
MI, transverse diameter.....	12.5
M2, antero-posterior diameter.....	30.8
M2, transverse diameter.....	11.8
	No. 2023
Phalanx I, length along median plane.....	92.5
Phalanx I, antero-posterior diameter at proximal end.....	25.5
Phalanx I, transverse diameter at proximal end.....	28.0
Phalanx I, antero-posterior diameter at distal end.....	21.0
Phalanx I, transverse diameter at distal end.....	25.0

(a) Approximate.

Pliomastodon? cosoensis n. sp.

Holotype—An incomplete skull, No. 1719 (Plate 5), from Calif. Inst. Vert. Pale. Loc. 284.

Paratype—A complete mandible, No. 1720 (Plate 6), from the same locality.

Referred Material—An immature palate, No. 2036 (Plate 7), and several isolated adult molars. All are from the same locality as the holotype.

Specific Characters—Size moderate; in this character *Pliomastodon? cosoensis* exceeds somewhat *P. nevadanus* from the Thousand Creek beds, but is considerably smaller than *P. vexillarius* from the upper Etchegoin. Upper tusks curve upward and outward much as in the latter species, and lack

¹ Chester Stock, Carnegie Inst. Wash. Pub. No. 393, pt. 4, 29-37, 1928.

² O. P. Hay, Proc. U. S. Nat. Mus., vol. 59, 622-626, 1922.

enamel bands. Cheek-teeth with a slight deposit of cement. M_2^2 with three transverse crests; M_3^3 with four transverse crests and a well-formed heel. Anterior margin of the posterior nares well back of the last upper molars.

Description—The skull, No. 1719, apparently belongs to a mature individual, for the last two molars are well worn. The space between the anterior margin of the posterior nares and the posterior borders of the last upper molars measures 52 millimeters. In this respect the Coso Mountains specimen differs markedly from both *P. vexillarius* and *P. nevadensis*, in which the nares are very nearly in line with the back of the tooth-row. It seems reasonable to infer that in No. 1719 the condyles were comparably farther back of the tooth-row than in either the upper Etchegoin or Thousand Creek specimens. The condition seen in the Coso specimen has been correlated by Gregory¹ with a shortened proboscis, shortened tusks, or both. Since the ends of the incisor tusks are missing in No. 1719, it is impossible to decide which may be considered here the more important. It is possible that the Coso specimen possessed a relatively short proboscis, but the extreme shortness of the symphysis does not suggest that this was the case. The tusks themselves are elliptical in cross-section, and show no trace of enamel bands except for a slightly roughened area on the outer side and near the base of the left tusk. As shown by Plate 5, the tusks curve gently upward and outward, but not to so great an extent as in *P. vexillarius*.

The upper teeth resemble those of *P. nevadensis* in the number of transverse crests, but differ markedly in details of tooth pattern. The more important differences are the lack of small tubercles between the principal cusps in the Coso Mountains material. In addition, M_3 shows the presence of trefoils on the inner cusps of the first three transverse crests, a feature not so well developed in the Nevada specimen.

The mandible, No. 1720, does not belong to the individual possessing the skull just described, as is evidenced by the less worn state of the dentition in the mandibular specimen. The lower jaw is remarkable for its extreme massiveness. Plate 6, figure A shows the great width of the horizontal ramus lateral to the tooth-row which gives the mandible this appearance. The symphysis is short as in *Mastodon americanus*, and shows no trace of lower tusks. It is possible, however, that the specimen No. 1720 represents a female.

The lower teeth are characterized by sharp-crested lophs with fairly open valleys between. M_2 is deeply worn, and all that can be determined is that it possessed three lophs with little indication of trefoils, except on the outer cusps of the first anterior loph. M_3 shows four full lophs which decrease progressively in width from the first to the fourth, and a fully formed heel. The latter is divided into two cusps of unequal size, the larger of which is situated on the outer border of the crown. Indications of trefoils appear on the outer cusps of the first three lophs, but except for a slight deposit of cement the valleys are otherwise open. The last lower molar is convex along the inner border, while the outer margin is nearly straight. A well-developed cingulum is present along the outer border of M_3 , but indications of an internal cingulum are lacking. Both the upper and lower molars are fairly high-crowned, as is shown by Plates 5 and 6. The lophs are directed almost vertically.

Dentition of Immature Individual—These teeth are of considerable interest in that they are seldom described in the literature. Reference to Plate 7

¹ W. K. Gregory, Bull. Amer. Mus., vol. 19, 387-394, 1903.

shows that Dp2 is nearly square in outline and divided into two transverse crests. Each crest is divided into two cusps, while the valley between the transverse crests is quite open. A fairly well-defined cingulum extends almost completely around the entire tooth.

Dp3 possesses two fully formed lophs with the third (posterior) one only partially developed. The lophs are divided into two separate cusps as in Dp2. The valley between the first and second lophs is nearly closed by the development of trefoils from the inner cusps of the first two transverse crests. There is also a trefoil on the anterior border of the inner cusp of the first transverse crest. There are faint indications of a cingulum around this tooth.

Dp4 is divided into three fully formed transverse crests. Well-defined trefoils occur on both the anterior and posterior margins of the inner cusps, but these seem to be absent on the outer cusps. A cingulum extends around this tooth to the posterior margin, where its presence cannot be determined, since this part of the crown has not emerged from the palate. All the teeth are fairly high-crowned, but show no indication of cement.

Remarks—Osborn¹ lists the characters of the genus *Pliomastodon* as follows: incisive tusks with enamel band vestigial or wanting, sub-oval to rounded in section, upturned (*P. vexillarius*); ridge-crests with expanded ectotrefoils (*P. matthewi*); intermediate in hypsodonty between *Miomastodon* and *Mastodon*. In his discussion of *P. vexillarius* this author adds the following generic characters: molar teeth wide, moderately crested, less so than in *Mastodon*, trefoils single, not prominent, valleys open, M2 trilophodont, M3 with four and one-half crests. The basicranial region of the skull is little elevated above the palatal plane, much shortened as compared with *Mastodon*, occiput very low and wide, heavily overhanging backward instead of nearly vertical as in *Mastodon* and other genera. Posterior nares crowded forward so as to be opposite the back of M3; in *Mastodon* they are considerably behind it. The entire basicranial region is thus crowded forward along with the condyles, which are scarcely more than half as far behind the teeth as in *Mastodon*.

On the basis of the above distinctions between *Pliomastodon* and *Mastodon*, there would appear to be good reason for regarding *P. cosoensis* as intermediate between these two genera, for while most of the characters shown by the Coso Mountains specimen agree very well with *Pliomastodon*, the position of the posterior nares is very similar to that seen in *Mastodon*. It is possible to regard the combination of characters shown by *P. cosoensis* as the basis of a new genus intermediate between *Pliomastodon* and *Mastodon*, but there appears to be little room for an intermediate genus between two such closely related groups. If this interpretation is correct, it would appear that the Coso Mountains specimen represents the most advanced species of the genus *Pliomastodon* yet described.

Measurements (in millimeters) of Pliomastodon? cosoensis n. sp.

No. 1719

Distance from back of upper tooth-row to anterior margin of posterior nares.....	52
Width of palate between the inner margin of M3 at the first loph.....	92
Transverse diameter of tusk at alveolus.....	78
Dorso-ventral diameter of tusk at alveolus.....	69
M2, antero-posterior diameter.....	92
M2, transverse diameter across third crest.....	59

¹ H. F. Osborn, *The Proboscidea*, 157, 162, New York, 1936.

Measurements (in millimeters) of Pliomastodon? cosoensis n. sp.—(Continued)

	No. 1719
M3, antero-posterior diameter.....	138
M3, transverse diameter across first crest.....	71
	No. 1720
Length of lower jaw from condyle to tip of symphysis.....	797
Length of lower jaw from back of M3 to tip of symphysis.....	470
Greatest width of lower jaw measured across second loph of M3.....	434
Width of lower jaw measured from the outer margin of the second loph of M3....	242
M2, antero-posterior diameter.....	99
M2, transverse diameter across third crest.....	71
M3, antero-posterior diameter.....	168
M3, transverse diameter across second crest.....	87
M3, height of second crest above valley.....	36
	No. 2036
Dp2, antero-posterior diameter.....	22.5
Dp2, greatest transverse diameter.....	19
Dp3, antero-posterior diameter.....	37
Dp3, greatest transverse diameter.....	33
Dp4, antero-posterior diameter.....	59
Dp4, greatest transverse diameter.....	46

Mimomys primus (Wilson)

A badly crushed skull with dentition, No. 500, Calif. Inst. Vert. Pale. Loc. 131, was designated as the type of the new genus, *Cosomys*.¹ Hinton² has given valid reasons for considering the type as identical with *Mimomys* of the later Cenozoic of the Old World, and would refer the Coso Mountains material to *M. phiocenicus*. Later, Wilson³ revised the characters of *M. primus*, and referred the Coso Mountains material to the European genus. Specimen No. 500 was distinguished from *M. phiocenicus* by the following characters: (1) absence of cement in the re-entrant folds; (2) lack of reduction of the tip of the second re-entrant angle on M3; and possibly (3) union of the temporal ridges in the Coso Mountains specimen.

Additional material now available comprises isolated teeth, and furnishes no further information regarding this form.

Hypolagus near limnetus Gazin

The lagomorphs in the collection have been studied by R. W. Wilson, who has kindly furnished the following descriptions:

Several lagomorph specimens are represented in the Coso Mountains collection. The material from locality 131 consists of a right ramus, No. 1978 (Plate 8, figs. 1, 1a), complete except for the ascending ramus; a fragment of left ramus with M2-M3, No. 1979; a fragment of maxillary with left M2-M3, No. 1980; and a few skeletal elements. The fossil remains appear to represent a species near *Hypolagus limnetus*.

The Coso Mountains leporid, although occurring in beds of approximately the same age as those at Hagerman, Idaho, yielding *H. limnetus* remains, is somewhat smaller than the type of the latter species. The ramus in No. 1978 is actually not so deep, but may be relatively, as in typical *H. limnetus*. On the other hand, the diastema between I and P3 is very slightly longer. The actual depth of ramus corresponds more closely to that in *H. furlongi*, a closely related type from Grand View, Idaho. P3 in the Coso Mountains form is quite close in characters to that of *H. limnetus*. The antero-external fold in the tooth is relatively deep, thus agreeing with

¹ R. W. Wilson, Jour. Mammalogy, vol. 13, 150-154, 1932.

² M. A. C. Hinton, Jour. Mammalogy, vol. 13, 280-281, 1932.

³ R. W. Wilson, Carnegie Inst. Wash. Pub. No. 440, pt. 8, 128, 1934.

the third premolar of the Hagerman species. However, the tooth may be slightly more narrow anteriorly, and the postero-external fold possesses a small plication on the anterior enamel face, a feature not recorded in the description of *H. limnetus*.¹ The presence of a similar plication in a specimen of *H. vetus*, in which species it is normally absent, indicates that in the above case no particular reliance can be placed on a single plication. The lower molariform teeth of *H. near limnetus* appear to be similar to those in the Hagerman type. In No. 1980 the enamel infold of M₂ is rather complexly plicated, probably agreeing more closely in this regard with *H. limnetus* than do specimens from the Kern River beds, referred to *H. near limnetus*.² Without actual specimens from Hagerman, certain other characters which have been cited for *H. limnetus* are difficult to check in our specimen.

Hypolagus furlongi Gazin³ from Grand View, although perhaps slightly larger than the Coso Mountains form, is apparently closer to it in size than is *H. limnetus*. However, in character of P₃, the Californian form is less triangular, more as in the Hagerman type, and the antero-external fold is deeper, again a character which is closer to that shown in *H. limnetus*. Moreover, the diastema between I and P₃ is distinctly shorter in the Grand View species. On the whole, the Coso Mountains leporid is closer to *H. limnetus* than to *H. furlongi*, and especially in regard to character of P₃. The slightly better agreement in size between No. 1978 and *H. furlongi* is probably of no great importance, since size must be a variable character to a certain extent, and the Coso Mountains material is limited in amount.

Hypolagus browni (Hay),⁴ compared with *H. near limnetus*, is recorded from a somewhat younger stage, namely early Pleistocene(?). The species is smaller than our form, No. 1978. A certain amount of variation in P₃ is seen in the Pleistocene type. However, this tooth appears to be more advanced in character of the postero-external fold than in our species. The antero-external fold of P₃ is shallower. M₂ appears to be less complexly plicated than in *H. near limnetus*.

Hypolagus vetus (Kellogg)⁵ is not at all close to the Coso Mountains species. It is much larger, and differs also in several characters in the dentition.

Hypolagus edensis Frick⁶ is readily distinguished from our form. The rounded internal borders of the lower molariform teeth, and perhaps the pronounced anterior position of the antero-external fold in P₃ as well, are characters which appear to be quite peculiar to *H. edensis*, if the type is correctly figured.

The Coso Mountains species is somewhat smaller than average specimens of *H. near limnetus* from the Kern River beds, although only slightly smaller than some specimens. The important third lower premolar is similar to that in the Kern River species, but in the latter the average P₃ is a little more rounded anteriorly, and the widest part of the tooth is slightly farther forward than in No. 1978. The only upper molariform tooth available for comparison is M₂. The anterior border of the median re-entrant fold of

¹ C. L. Gazin, Proc. U. S. Nat. Mus., vol. 83, no. 2976, 114-117, figs. 2-3, 1934.

² R. W. Wilson, Carnegie Inst. Wash. Pub. No. 487, pt. 1, 1-19, 1937.

³ G. L. Gazin, *op. cit.*, 118-119, fig. 4, 1934.

⁴ O. P. Hay, Proc. U. S. Nat. Mus., vol. 59, 630-631, pl. 121, figs. 6-18, 1921.

⁵ L. Kellogg, Univ. Calif. Pub., Bull. Dept. Geol., vol. 5, no. 29, 436-437, fig. 20, 1910.

L. R. Dice, Univ. Calif. Pub., Bull. Dept. Geol., vol. 10, no. 12, 181-182, figs. 4-5, 1917.

⁶ C. Frick, Univ. Calif. Pub., Bull. Dept. Geol., vol. 12, no. 5, 348, fig. 52, 1921.

this tooth appears to be slightly more complexly plicated in the Coso Mountains type.

It is doubtful if *H. near limnetus* from the Kern River beds is conspecific with *H. near limnetus* from the Coso Mountains, but each one is probably closer to typical *H. limnetus* than to any other species of *Hypolagus*. It may be that the Kern River form represents a distinct species. Probably the Coso Mountains species is merely a small individual of typical *H. limnetus*. In any case, in view of the number of species of *Hypolagus* already distinguished, nothing is gained by a further separation of types.

Measurements (in millimeters) of Hypolagus near limnetus Gazin

No. 1978

P3-M3, alveolar length.....	11.9
P3-M3, occlusal length.....	10.7
Depth of ramus beneath M1, measured from inside.....	10.8
Length of diastema between I and P3.....	13.4—

Hypolagus small sp.

Two lagomorph specimens, Nos. 2026, 2027, from locality 131 in the Coso Mountains, are much smaller than other hare material obtained from this locality. The more complete specimen consists of a right ramus, No. 2026 (Plate 8, figs. 2, 2a), with P3-M3 inclusive. No. 2027 represents an isolated left P2. Not only does this material differ from *Hypolagus near limnetus* in smaller size, but also P3 of No. 2026 has a less deeply folded antero-external inflection, and M3 is more reduced, exhibiting a single column indented at its postero-external margin. M3 of *H. near limnetus* shows the usual double column of *Hypolagus*.

In size, *Hypolagus small sp.* is much smaller than most species of the genus. P3 is somewhat quadrilateral in outline, and hence is relatively broad transversely. The posterior portion of the internal surface of the tooth is flattened. P3 exhibits a postero-external inflection extending slightly more than half-way across the surface of the tooth, and a shallow but distinct antero-external fold of enamel. The anterior surface of the tooth is slightly indented, suggesting a very shallow and broad inflection of enamel. The anterior and posterior columns of P4-M2 are subequal in transverse width, but the latter are slightly shorter in this dimension with respect to the anterior ones. M3 shows a simple, somewhat obliquely elliptical column with a single fold as indicated above. P2 has an anterior fold on the occlusal surface of the tooth. The slight antero-external fold usually present in *Hypolagus* is absent, although inspection of the anterior lateral wall of the tooth indicates the probable presence of a slight fold upon further wear.

Hypolagus edensis, *H. ? apachensis*, and *H. browni* approach No. 2026 more closely in respect to size than do other species of *Hypolagus*. *H. browni* (Hay)¹ is comparable to *Hypolagus small sp.* in size, although judging from figures of the former given by Hay and Dice, the tooth-row is very slightly longer in the Arizonan species, and the ramus somewhat heavier. P3 of *H. browni* differs perhaps in having a more complex posterior enamel fold,

¹ O. P. Hay, *op. cit.*, 630-631, pl. 121, figs. 6-18, 1921.

L. R. Dice, *Papers Mich. Acad. Sci., Arts, and Letters*, vol. 16, 379-382, figs. 8-10, 1932.

C. L. Gazin, *op. cit.*, 116-117, 1934.

although it is difficult to ascertain how much this character in *H. browni* depends on stage of wear. $M\overline{3}$ of the Coso Mountains type is unlike Hay's species in exhibiting a single column. In character of this tooth, No. 2026 is similar to most specimens of *Palæolagus*. In more modern types of lagomorphs, simple third lower molars appear to be at least relatively rare. The assumption can be made that character of $M\overline{3}$ in No. 2026 is the result of advanced wear, but definite proof is lacking until more specimens are available.

Hypolagus edensis (Frick) ¹ as compared with the Coso Mountains species is larger, and possesses a $P\overline{3}$ in which the antero-external inflection is deeper, and more anterior in position. Moreover, $P\overline{4}$ and $M\overline{1}$ in *H. edensis* exhibit rounded internal borders lacking the angulation shown in these teeth in No. 2026.

Hypolagus? apachensis Gazin ² is from a distinctly older geological stage. $P\overline{3}$ is more elongated antero-posteriorly than in *Hypolagus* small sp. $P\overline{2}$ normally has two anterior folds of enamel. Lastly, *H.? apachensis* is distinctly larger than the Coso Mountains form.

Hypolagus sp. from Rome and *Hypolagus* small sp. from the Kern River deposits both differ from No. 2026 in larger size. In addition, the Kern River type possesses a $P\overline{3}$ which is more elongated antero-posteriorly.

Other species of *Hypolagus* are much larger than the Coso Mountains species, and generally differ in one or more additional characters as well.

The Coso Mountains species is clearly distinct from all described species of North American *Hypolagus* except possibly *H. browni*. If supplementary material of the California species were to reveal a constancy of the characters exhibited by the present remains, establishment of a new species would seem to be warranted. Without other specimens, however, it is perhaps best to refrain from giving a specific designation to this Coso Mountains lagomorph.

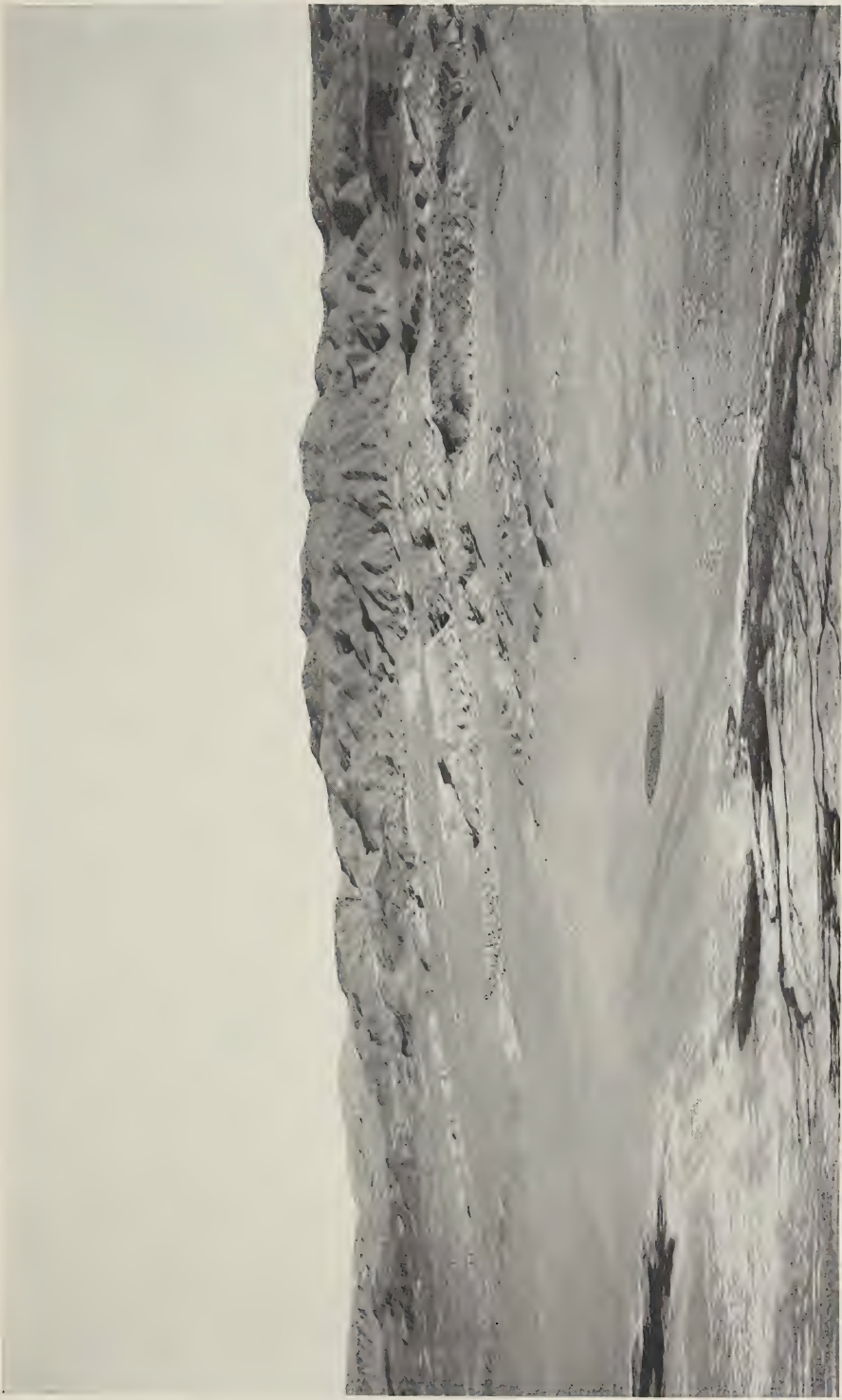
Measurements (in millimeters) of Hypolagus small sp.

	No. 2026
$P\overline{3}$ - $M\overline{3}$, alveolar length.....	9.7 (a)
$P\overline{3}$ - $M\overline{3}$, occlusal length.....	7.7
Depth of ramus beneath $M\overline{1}$, measured from inside.....	7.3
Length of diastema between \overline{I} and $P\overline{3}$	9.0

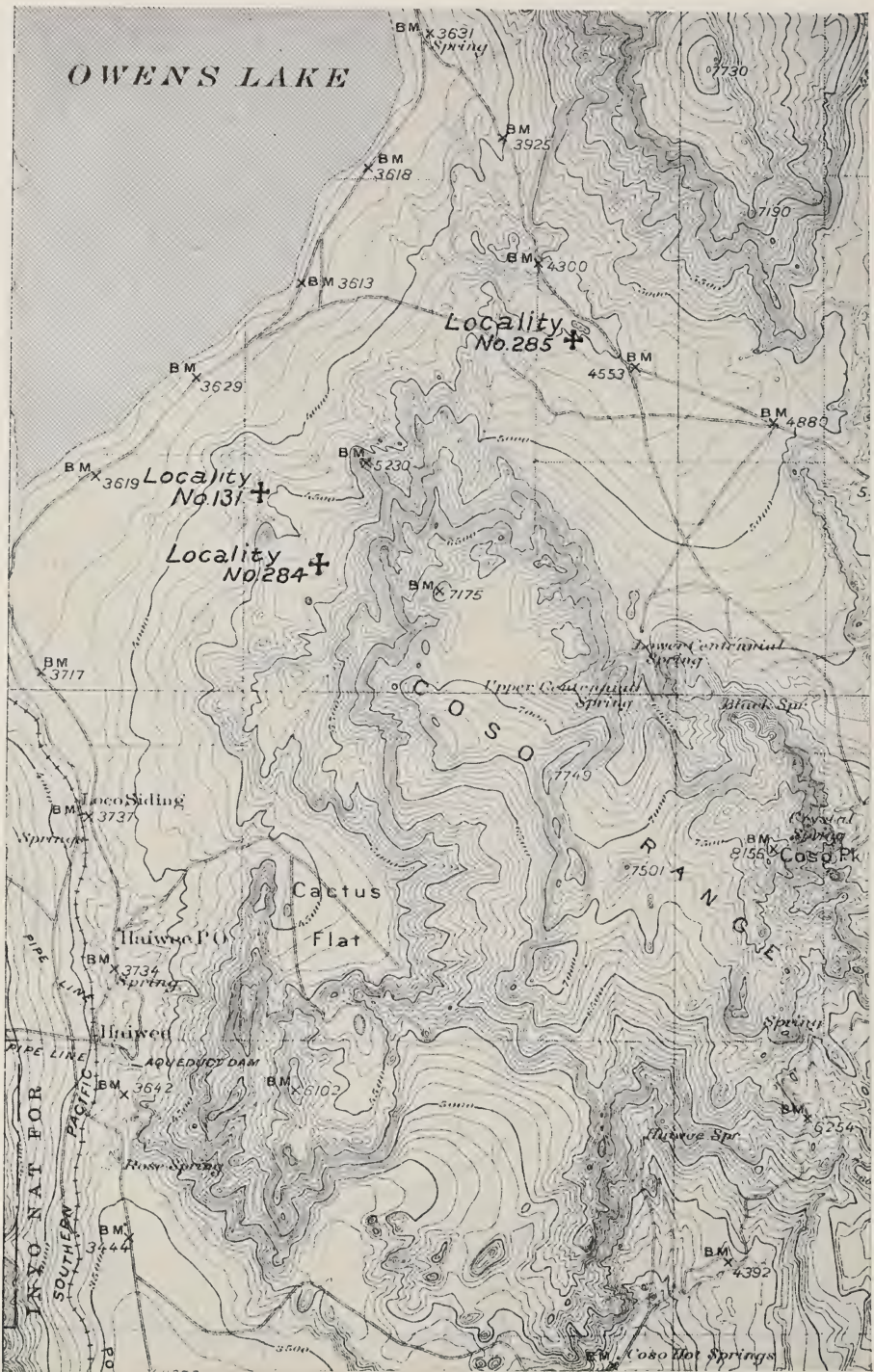
(a) Approximate.

¹ C. Frick, *op. cit.*, 348, fig. 52, 1921.

² C. L. Gazin, Carnegie Inst. Wash. Pub. No. 404, pt. 6, 67-69, pl. 3, figs. 1-4, 1930.



Aerial photograph of the northwestern flanks of the Coso Mountains, California. The crest of the range is made up of granite; light-colored sediments in foreground represent the Coso formation. Darker-colored lava flows which cover both the granite and the sediments are seen at extreme right and left. Fossil localities 131 and 284 are located in the upper reaches of the large wash in the middle foreground.



Southwestern portion of the U. S. Geological Survey Ballarat Quadrangle showing the location of the California Institute vertebrate fossil localities in the Coso Mountains. Scale 1:250,000, contour interval 100 feet.



Plesippus francescana (Frick)

Skull No. 2020, Calif. Inst. Loc. 284, dorsal and ventral views. Approx. $\times \frac{1}{4}$. J. L.
Ridgway *del.*
Late Cenozoic, Coso Mountains, California.



Plesippus francescana (Frick)

A—No. 2021, Loc. 131, mandible. Approx. $\times \frac{1}{2}$.

B—No. 2016, Loc. 131, palate. Approx. $\times \frac{1}{2}$.

Calif. Inst. Tech. Vert. Pale. Coll. Late Cenozoic, Coso Mountains, California.



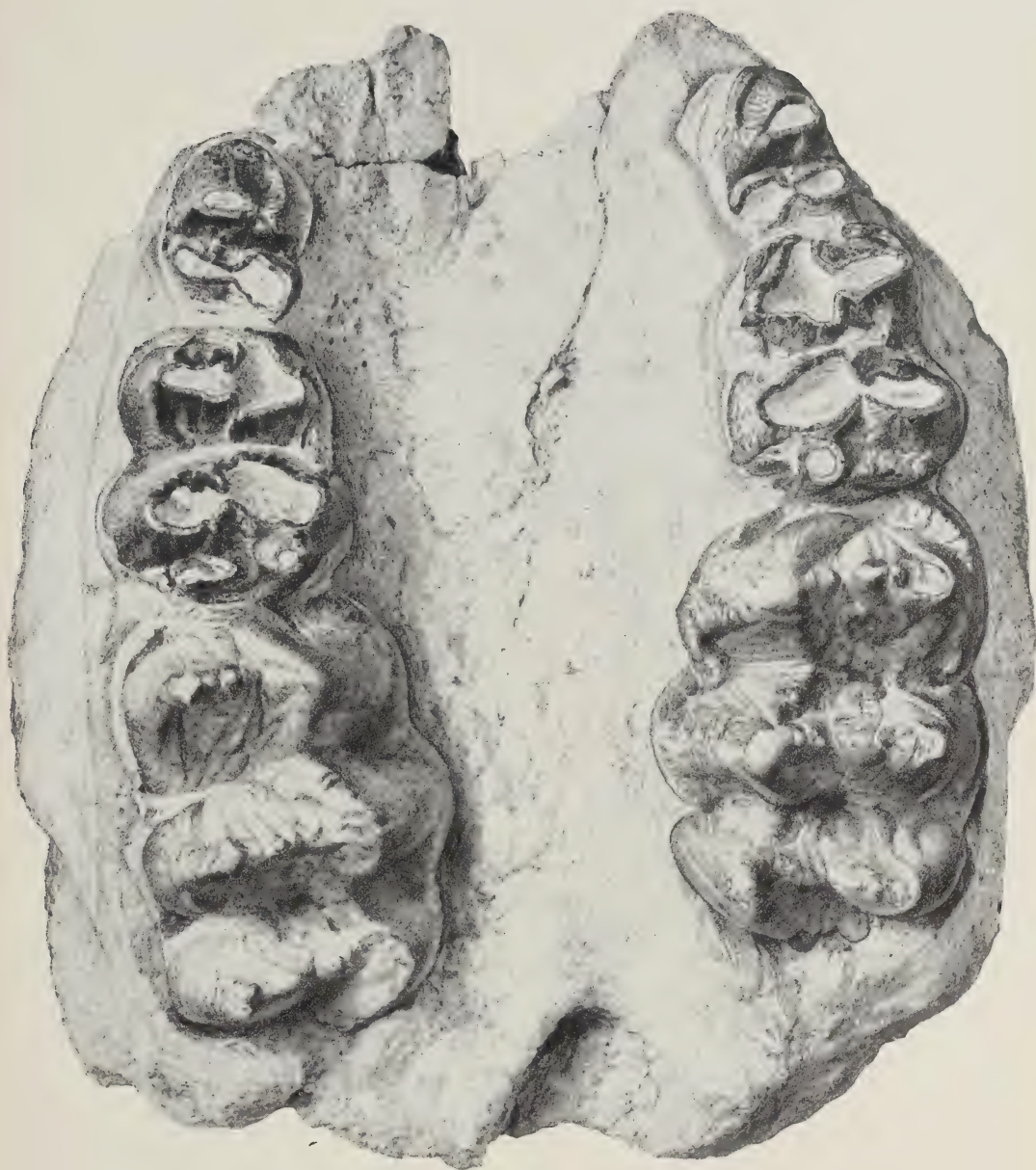
Pliomastodon? cosoensis n. sp.

No. 1719, Loc. 284, skull, occlusal and lateral views. Approx. $\times 1/6$.
Calif. Inst. Vert. Pale. Coll. Late Cenozoic, Coso Mountains, California.



Pliomastodon? cosoensis n. sp.

No. 1720, Loc. 284, mandible, occlusal and lateral views. Approx. $\times 1/7$.
Calif. Inst. Tech. Vert. Pale. Coll. Late Cenozoic, Coso Mountains, California.



Pliomastodon? cosoensis n. sp.

No. 2036, Loc. 284, palate of an immature individual with Dp₂-Dp₄. × 1.
Calif. Inst. Tech. Vert. Pale. Coll. Late Cenozoic, Coso Mountains, California.



FIG. 1—*Hypolagus* near *limnetus* Gazin. No. 1978, right ramus, lateral view. $\times 2$.
 FIG. 1a—*Hypolagus* near *limnetus* Gazin. No. 1978, right ramus, dorsal view. $\times 3$.
 FIG. 2—*Hypolagus* small sp. No. 2026, right ramus, lateral view. $\times 4$.
 FIG. 2a—*Hypolagus* small sp. No. 2026, right ramus, occlusal view. $\times 4$.
 FIG. 3—*Platygonus* sp. No. 1850c, M3. $\times 2$.
 FIG. 4—*Platygonus* sp. No. 1850a, M1? $\times 2$.
 FIG. 5—*Platygonus* sp. No. 1850b, M1? $\times 1$.
 FIG. 6—*Platygonus* sp. No. 1850, anterior portion of mandible. $\times 1$.
 Sizes of all figures approximate.
 Calif. Inst. Tech. Vert. Pale. Loc. 131. Late Cenozoic, Coso Mountains, California.

CONTRIBUTIONS TO PALÆONTOLOGY

IV

A LATE QUATERNARY MAMMAL FAUNA FROM THE
TAR SEEPS OF MCKITTRICK, CALIFORNIA

By JOHN R. SCHULTZ

With seventeen plates and twelve text-figures

[Issued July 6, 1938]

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A LATE QUATERNARY MAMMAL FAUNA FROM THE TAR SEEPS OF MCKITTRICK, CALIFORNIA

INTRODUCTION

Because of their many unusual features vertebrate fossil occurrences in tar beds of California have aroused much interest. Rancho La Brea is perhaps the most widely known fossil locality in the world, while the work of Chaney and Mason (1933), L. H. Miller and A. H. Miller (1931, 1932), and Wilson (1933) has established for Carpinteria a well deserved place in the literature of palæobotany and palæontology. Although numerous short papers dealing with various aspects of the fauna of McKittrick, western Kern County, California, have appeared in times past, the mammalian assemblage as a whole has not been described, and this is the primary purpose of the present report. While major emphasis is placed upon the mammals, opportunity is taken to supplement the record of this group with a brief review of the avian and plant assemblages. The combined evidence is discussed in relation to that of Rancho La Brea and Carpinteria, and an effort is made to determine the time sequence of these three asphalt deposits.

In a region so topographically and climatically varied as California, distribution of fossil forms in both time and space must be known before satisfactory correlations can be made. Rancho La Brea furnishes an unparalleled record of late Pleistocene life of the Los Angeles Basin, while Carpinteria is most noteworthy for its plant record of this period. The caves in the mountainous northern and middle parts of the state have furnished large and varied faunas, but their time relations to the tar pit assemblages are difficult to determine.

Owing to its geographic position, the McKittrick fauna is of considerable importance, and for the first time an adequate record of late Pleistocene life of the San Joaquin Valley is available. The information now at hand seems to indicate that no very significant time difference exists between the three asphalt faunas, but a correlation of these assemblages with those of the California caves still remains as an important problem requiring solution. Of greater importance is the correlation with faunas from other parts of North America and with those of the Old World. When such studies are completed, the tar bed assemblages will be found to possess fundamental significance.

So unlike the existing fauna of California are the asphalt assemblages that it is not difficult to understand why early workers were inclined to regard the latter as dating from the early Pleistocene. While

abundance of extinct forms indicates considerable antiquity measured in terms of years, it now appears that this criterion alone does



FIG. 1—Outline map of western United States showing location of Pleistocene vertebrate localities of California.

- | | |
|-------------------|----------------------|
| 1. McKittrick | 4. Hawver Cave |
| 2. Carpinteria | 5. Samwel Cave |
| 3. Rancho La Brea | 6. Potter Creek Cave |

not necessarily point to an age more remote than the latter part of the Glacial Period. Gradually it is becoming evident that the changes

which have brought about so great an impoverishment in mammalian life are of relatively recent date in the geological sense. Hardly less true for vertebrate palæontology than for geology are Gilbert's words: "When the work of the geologist is finished and his final comprehensive report written, the longest and most important chapter will be upon the latest and shortest of the geologic periods."

ACKNOWLEDGMENTS

The writer has been fortunate to carry out this work under the supervision of Dr. Chester Stock, who not only aided in every possible way but, by his unfailing interest, furnished a constant source of encouragement. R. W. Wilson gave generously of his time and knowledge in the determination of the rodents and lagomorphs in the McKittrick collection. E. L. Furlong, to whom has fallen the task of preparing much of the material, furnished many valuable suggestions which are deeply appreciated. Those portions of the present report dealing with the avifauna have been read by Dr. Hildegarde Howard, and whatever merit they may possess is largely due to her careful and critical notations.

The Los Angeles Museum kindly permitted access to the Rancho La Brea collection; while the staff in charge of the Dickey collection of Recent mammals loaned important comparative material. The staff of the Museum of Palæontology, University of California, placed the McKittrick collection of that institution at the writer's disposal, and thus made possible a complete study of the fauna. I am particularly indebted for many courtesies to R. A. Stirton, V. L. Vander Hoof, and C. J. Hesse. Dr. Joseph Grinnell of the Museum of Vertebrate Zoology, University of California, permitted access to the collections of Recent mammals. Dr. W. S. W. Kew of the Standard Oil Company of California made available a geological map of the McKittrick area, while V. L. Vander Hoof furnished a detailed topographic and geologic map of the same area. Dr. Vander Hoof also loaned maps and photographs of the brea deposits, and furnished detailed information based upon his own studies of the McKittrick tar seeps.

John L. Ridgway prepared the illustrations and retouched the photographs. Other acknowledgments of assistance are made in the text.

HISTORICAL REVIEW

A summary of the results of previous workers is necessary in order to place the present study in proper perspective.

First mention of vertebrate remains from the McKittrick region seems to have been made by Joseph Leidy (1865, p. 94), who described

two horse teeth from the vicinity of Buena Vista Lake and referred them to *Equus occidentalis*. Additional horse material from this locality was described and figured by Leidy in 1873 (pp. 242-244, pl. 33, fig. 1). Whitney (1880, p. 256) stated that Leidy's specimens were obtained from Santa Maria Oil Springs, a locality approximately two miles to the southwest of McKittrick.

Although Watts (1894, pp. 46-50) treated the asphaltum from an economic point of view, for a period of nearly twenty-five years no further interest seems to have been manifested in the palæontology of the locality.

In 1903 J. C. Merriam (1903, pp. 288-289, pl. 30, fig. 2) described a fragmentary lower jaw of *Canis indianensis* from a locality given as Oil Springs in Tulare County. Doubt was expressed as to the occurrence of this find in Tulare County, for the Asphalto area, a short distance east of McKittrick, was at that time known as Oil Cañon. In the same paper *Hyænognathus pachyodon* was described by Merriam. The type of this genus came from beds of either late Pliocene or early Quaternary age situated near Asphalto. Two years later, the same author (Merriam, 1905) described from the Asphalto deposits an extinct feline type now known as *Ischyrosmilus ischyurus*. The Asphalto fauna served to revive palæontological interest in the region, but the assemblage is not closely related to that of McKittrick.

In 1908 F. M. Anderson (pp. 32-33) described a series of upraised Pleistocene terraces in the McKittrick area. Mention was also made of extensive beds of asphalt in which were found remains of elephants, horses, and an extinct species of wolf. The fauna was thought to belong to the latter part of the Pleistocene period.

Six years later, at the suggestion of J. C. Merriam, Neil Cornwall made a reconnaissance of the Asphalto and McKittrick areas. Although a part of the summer was spent in this work, the information obtained at that time was never published.

In 1921 construction of the Taft-McKittrick paved highway brought to light a fossiliferous bed of asphalt on the southern outskirts of McKittrick. The occurrence was reported by Merriam and Stock (1921), and eleven mammalian forms were listed: *Ænocyon dirus*, *Canis* near *ochropus*, *Felis atrox*, *Felis* near *daggetti*, *Arctotherium* near *simum*, *Myiodon* sp., *Equus occidentalis*, *Antilocapra?* sp., *Bison* sp., a slender-limbed camel, and *Mastodon* sp. The birds were studied by L. H. Miller, who found ten species in all, six of which are aquatic or semi-aquatic in habit. Shore birds, which are rare at Rancho La Brea, appeared to be very abundant at McKittrick. At this time Merriam and Stock were inclined to attribute the dissimilarities between the McKittrick and Rancho La Brea assemblages to

environmental factors, although an age difference between the two deposits was considered a possible contingency.

In the following year Miller (1922) published a preliminary report on the McKittrick birds. At that time the collection numbered approximately 325 specimens. Two years later the same author (Miller, 1924) noted the absence of gulls at McKittrick and their rarity at Rancho La Brea. It was concluded that these birds were late-comers on the California coast.

Charles H. Sternberg began collecting at McKittrick in 1925 and continued his excavations until 1927. During this time most of the material now in the collections of the California Institute of Technology was obtained. An interesting account of Sternberg's work is to be found in the book "Hunting Dinosaurs" (Sternberg, 1932, pp. 242-252).

In 1925 L. H. Miller (pp. 307-326) published another important paper on the McKittrick birds. This report was based on a study of approximately 1000 specimens, representing thirty-four species. Of these eighteen were assigned to living species, while four were referred tentatively to forms still extant. Seven types were not specifically determined. Three species were thought to be extinct, while two were found to live no longer in the region. Remains of water birds were stated to outnumber those of land forms approximately two to one. Ducks and shore birds predominated. Migratory species were thought to form a larger percentage of the fauna than at Rancho La Brea. No evidence was found of gulls, divers, steganopods, night herons, condors, and small vultures. The golden eagle appeared to be the most abundant species. As a whole the bird assemblage was regarded as indicative of a marshy country with water only in small and shallow bodies, but not in true lakes. Miller suggested that the avifauna might indicate a somewhat later age than the Rancho La Brea and Fossil Lake assemblages.

During the same year Stock (1925, pp. 202-203) published a monograph on the gravi-grade edentates. In this work the 1921 mammalian faunal list was enlarged to include the badger, *Taxidea* sp. The proboscidean formerly described as *Mastodon* sp. was listed as *Mammot* near *americanum*. Considerable emphasis was placed upon the reported absence of *Smilodon* from the McKittrick locality, and absence of the slender-limbed camel at Rancho La Brea. The camel was thought to be generically distinct, and closely related to *Lama*. It was concluded from evidence furnished by the birds and mammals that the conditions of life during the Pleistocene were different at McKittrick and Rancho La Brea. Possibility of an age difference between the two faunas, however, was not considered as out of the question.

In a paper by Merriam and Stock (1925), the large camel, *Camelops* sp., was added to the faunal list. In the same publication (Merriam and Stock, 1925A) the slender-limbed camel was described as *Lama stevensi*.

Two years later Stock and Furlong (1927) announced the discovery in the McKittrick tar seeps of a musk-ox-like animal, which they tentatively referred to as *Preptoceras sinclairi*. At this time these authors were inclined to believe that faunal differences between McKittrick and Rancho La Brea could not wholly be accounted for by geographic separation. Consequently, the two asphalt occurrences could hardly be contemporaneous.

During the same year Hay's (1927, pp. 197-199) comprehensive work on the Pleistocene vertebrates appeared. The 1925 mammalian and avian faunal lists were reprinted, and the combined evidence summarized. Hay concluded that any differences between McKittrick and Rancho La Brea must be due to environmental factors, for in the opinion of that author, both assemblages are of Aftonian age.

In 1928 Stock (pp. 25-27) described some fragmentary peccary remains from the McKittrick asphalt, and referred them to *Platygonus* near *compressus*. In the same publication (Stock, 1928A) *Lama stevensi* was designated the type of a new genus, *Tanupolama*. *Camelus americanus* from the Pleistocene of Hay Springs, Nebraska, was found to be referable to the new genus.

The faunal list was still further extended in 1930, when Furlong (pp. 49-53) described *Capromeryx minor* from McKittrick.

Two years later Merriam and Stock (1932, pp. 225-226) made important additions to the McKittrick Felidæ. *Smilodon californicus* was recorded from the locality for the first time; while mention was made of a wildcat, but without specific designation. The McKittrick puma was compared with *Felis bituminosa* and *Felis daggetti*, and the conclusion was reached that it is more closely related to the latter. It was observed, moreover, that the larger cats in the McKittrick collections do not dominate in numbers the puma and wildcat to the extent seen at Rancho La Brea. The suggestion was made that in the McKittrick fauna, *Felis atrox* may have outnumbered *Smilodon*.

In 1934 V. L. Vander Hoof (p. 332) published a brief account of the geology of the McKittrick fossil occurrence. It was pointed out that the tar seeps have their origin in fissures which cut the underlying oil sands. Alternate banding of tar and alluvium was interpreted as due to seasonal changes in temperature. It was thought that in summer the tar becomes fluid enough to spread over relatively large areas; while the winter rains were considered sufficient to wash in large quantities of alluvium. A sequence of 180 bands was counted and plotted. A correlation with the tree ring and varve chronologies

has been attempted, but this part of the study has not as yet been published.

One year later another paper by L. H. Miller appeared (1935). In this important contribution to the McKittrick avifauna a collection of 3000 specimens was described. This assemblage was obtained from a locality on the south side of the Taft-McKittrick highway, and approximately one hundred feet from the original excavations on the opposite side of the road. The avifauna from the new locality was found to present some marked contrasts with assemblages described in earlier papers. In the assemblage from the south side of the highway flesh-eating birds were found to predominate. In Miller's opinion the difference between the two McKittrick avifaunas is not to be attributed to a time factor, but to difference in environment. The locality on the north side of the road was thought to mark the shore of a large lake; while the occurrence one hundred feet to the south was conjectured to have been mainly dry land. The striking similarity of the avifauna from the south side of the highway to that of Rancho La Brea was noted.

During the same year Ross (1935) proposed the name *Anabernicula* for a new genus of pigmy goose from the McKittrick asphalt. One of the two "pigmy geese" from Rancho La Brea cited as *Branta?* sp., and two specimens from McKittrick formerly referred to *Chen hyperborea* were assigned to the new genus. *Branta minuscula* from the late Pliocene or early Pleistocene of Arizona was found to be very close to *Anabernicula*.

Howard (1936, pp. 34-35) has since demonstrated that Ross's species and *Branta minuscula* are the same. However, this author is also of the opinion that the Arizona material represents a new genus. *Anabernicula gracilente* Ross thus becomes a synonym of *A. minuscula* (Wetmore).

By 1935 seventeen species of mammals from the McKittrick asphalt had either been listed or described, in addition to a larger number of birds. The general similarity of the fauna to that of Rancho La Brea was recognized, and outstanding dissimilarities were attributed either to environmental factors or to a time difference between the two assemblages.

The present study deals mainly with the mammals. Every effort has been made to complete the study of this group insofar as it is represented in collections now available at the California Institute of Technology and at the University of California, but the rodents in the latter collection have not been carefully examined. This part of the fauna is being studied by J. W. Paxton, who plans to publish a report in the near future. Continued collecting at McKittrick may bring new forms to light, so that no claim to finality is made in this

report on the fossil mammals. A considerable number of bird bones still awaits study, as does also a small assemblage of insects. Some fragmentary plant material is likewise available. The present paper is in many respects a synthesis, but in addition to the new species that is described many forms are listed from the area for the first time.

GEOGRAPHIC POSITION AND EXISTING PHYSICAL CONDITIONS IN THE McKITTRICK AREA CONTRASTED WITH THOSE AT RANCHO LA BREA

As is shown in figure 1, McKittrick is located approximately 120 miles north and slightly west of Los Angeles. The fossil deposit is situated in the foothills of the southern California Coast Ranges near the southwestern border of the San Joaquin Valley, an almost featureless plain which occupies the entire central portion of the state. To the south the Tehachapi and San Gabriel Mountains effectively isolate the region from the Los Angeles Basin and the Rancho La Brea area; while to the east the Sierra raise a formidable barrier between the San Joaquin Valley and Great Basin.

Rancho La Brea is located in the northwestern part of Los Angeles, and nearly three miles from the steep southern front of the Santa Monica Range. The Los Angeles Plain, in which this deposit is situated, is an area almost as featureless as the San Joaquin Valley. Since during the period of fossil accumulation configuration of major relief features was probably similar to that of the present day, it seems reasonable to infer that at that time climatic and life zones were also similarly demarcated.

The Temblor Range, which rises just to the west of McKittrick, is a broad belt of rugged upland country very similar in general appearance to the Santa Monica Mountains in the vicinity of Rancho La Brea. In summer these heights are somewhat cooler than the surrounding lowlands, while in winter the summits are often snow-covered. It is worthy of note, however, that snow is more frequent and somewhat more abundant on the Temblor than on the Santa Monica Range.

By virtue of its geographic position, the Rancho La Brea area enjoys an almost mediterranean climate. The rainfall is light, and is almost completely confined to the winter months. Fog is common on the slopes of the Santa Monicas, and in the Los Angeles Basin.

The climate of the McKittrick area, on the other hand, is somewhat more of a continental type, for while this area is likewise semi-arid, the summers are hotter and the winters colder than is usual in the Los Angeles district. It is difficult to estimate the effect a period of glaciation might have upon the climates of the two areas, and while fuller discussion must be left to a later page, it seems reasonable to

assume that the McKittrick area was more noticeably affected by such a change than the Los Angeles region. Could this assumption be proved, it might be possible to state with greater definiteness than is now possible, the time relations of the three asphalt faunas.

EXISTING LIFE OF THE MCKITTRICK AND RANCHO LA BREA AREAS

In uncultivated areas both the San Joaquin Valley and Los Angeles Basin support a sparse growth of vegetation of a semi-arid type. The Santa Monica Mountains, however, are covered by a substantial growth of brushy plants. On the crest and southern slopes chaparral is so dense as to be almost impenetrable. Some areas are covered with grass, sage, black walnut, and oak. The bottoms of the deeper canyons are heavily wooded with oak and a variety of shrub-like undergrowth. Occasional sycamores are present. The Temblor Range, on the other hand, supports only a sparse vegetation of brush and occasional stunted trees. This observation is of interest in that, as will be seen in later pages, there is evidence that during the period of fossil accumulation the Temblor Range was covered by a somewhat heavier growth of vegetation.

The *Atriplex* belt of the San Joaquin Valley does not at present extend into the region of McKittrick. This plant, however, is found at slightly lower altitudes and within a few miles of the fossil deposit. Since distribution of *Atriplex* seems to exercise an important influence upon distribution of rodents and passerine birds, this fact is of considerable significance.

Although Man's occupancy of both areas has disturbed considerably the native animal life, information is available as to at least some of the original faunal features of these regions. The wildcat still lingers in less frequented spots of the Santa Monica Mountains, while the Mexican jaguar has been reported by Indians as having been seen in the Temblor Range. The fauna of the San Joaquin Valley is essentially that of a semi-arid plain and is characterized by an abundance of kangaroo rats of the genus *Dipodomys*. Despite the relative dryness of the region, the marshes of Buena Vista Lake are still a favorite retreat for ducks and other water birds. As will be seen in later pages, similar conditions may have existed in the McKittrick area during late Pleistocene time.

GEOLOGIC RELATIONS OF THE MCKITTRICK BREA DEPOSITS

The geology of the McKittrick area has been discussed by Arnold and Johnson (1910, pp. 110-114, pl. 1), Pack (1920, pp. 20-61), and at a later time by Cunningham and Kleinpell (1934, p. 799, fig. 4).

TABLE 1—Recent mammalian fauna of the McKittrick area*

Temblor Range	San Joaquin Valley
TALPIDÆ	
Scapanus latimanus occultus Grinnell & Swarth (Southern Calif. Mole)	Scapanus latimanus occultus Grinnell & Swarth
SORICIDÆ	
Sorex ornatus ornatus C. H. Merriam (Adorned Shrew)	Sorex ornatus ornatus C. H. Merriam
	Sorex ornatus relictus Grinnell (Buena Vista Lake Shrew)
VESPERTILIONIDÆ	
Myotis yumanensis sociabilis H. W. Grinnell (Tejon Yuma Bat)	Myotis subulatus melanorhinus (C. H. Merriam)
Myotis subulatus melanorhinus (C. H. Merriam) (Black-nosed Bat)	Eptesicus fuscus (Peale & Beauvois)
Eptesicus fuscus (Peale & Beauvois) (Large Brown Bat)	Nycteris borealis teliotis (H. Allen) (Western Red Bat)
Nycteris cinerea (Peale & Beauvois) (Hoary Bat)	Nycteris cinerea (Peale & Beauvois)
Corynorhinus rafinesquii intermedius H. W. Grinnell (Intermediate Lump-nosed Bat)	Corynorhinus rafinesquii intermedius H. W. Grinnell
Antrozous pallidus pacificus C. H. Merriam (Pacific Pallid Bat)	Antrozous pallidus pacificus C. H. Merriam
MOLOSSIDÆ	
Tadarida mexicana (Saussure) (Mexican Free-tailed Bat)	Tadarida mexicana (Saussure)
	Eumops perotis californicus (C. H. Merriam) (Calif. Mastiff Bat)
URSIDÆ	
Ursus tularensis C. H. Merriam (Tejon Grizzly)	Ursus colusus C. H. Merriam (Sacramento Grizzly)
PROCYONIDÆ	
Procyon lotor psora Gray (Calif. Coon)	Procyon lotor psora Gray
MUSTELIDÆ	
Lutra canadensis brevipilosus Grinnell (Calif. River Otter)	Mustela xanthogenys xanthogenys Gray (Calif. Weasel)
Spilogale gracilis phenax C. H. Merriam (Calif. Spotted Skunk)	Lutra canadensis brevipilosus Grinnell
Mephitis mephitis holzneri Mearns (Southern Calif. Striped Skunk)	Spilogale gracilis phenax C. H. Merriam
Taxidea taxus neglecta Mearns (California Badger)	Mephitis mephitis holzneri Mearns
	Taxidea taxus neglecta Mearns

* Faunal list from Grinnell (1933).

TABLE 1—Recent mammalian fauna of the McKittrick area*—Continued

Temblor Range	San Joaquin Valley
CANIDÆ	
Urocyon cinereoargenteus californicus Mearns (Calif. Gray Fox)	Vulpes macrotis mutica C. H. Merriam (San Joaquin Valley Kit Fox)
Canis latrans ochropus Eschscholtz (California Valley Coyote)	Urocyon cinereoargenteus californicus Mearns
	Canis latrans ochropus Eschscholtz
FELIDÆ	
Felis concolor californica May (Calif. Mountain Lion)	
?Felis onca hernandesii (Gray) (Mexican Jaguar)	
Lynx rufus californicus Mearns (California Wildcat)	
SCIURIDÆ	
Citellus beecheyi beecheyi (Richardson) (Beechey Ground Squirrel)	Citellus beecheyi beecheyi (Richardson)
Citellus beecheyi fisheri (C. H. Merriam) (Fisher Ground Squirrel)	Citellus beecheyi fisheri (C. H. Merriam)
Ammospermophilus nelsoni nelsoni (C. H. Merriam) (Nelson Antelope Ground Squirrel)	Ammospermophilus nelsoni nelsoni (C. H. Merriam)
Eutamias merriami merriami (Allen) (Merriam Chipmunk)	Eutamias merriami merriami (Allen)
GEOMYIDÆ	
Thomomys bottæ pascalis C. H. Merriam (Fresno Pocket Gopher)	Thomomys bottæ pascalis C. H. Merriam
Thomomys bottæ diaboli Grinnell (Diablo Pocket Gopher)	Thomomys bottæ ingens Grinnell (Buena Vista Lake Pocket Gopher)
HETEROMYIDÆ	
Perognathus longimembris longimembris (Coues) (Tejon Pocket Mouse)	?Perognathus longimembris longimembris (Coues)
?Perognathus inornatus neglectus Taylor (McKittrick Pocket Mouse)	Perognathus inornatus neglectus Taylor
Perognathus inornatus inornatus C. H. Merriam (San Joaquin Pocket Mouse)	Perognathus inornatus inornatus C. H. Merriam
Perognathus californicus ochrus Osgood (Kern Calif. Pocket Mouse)	Perognathus californicus ochrus Osgood
Dipodomys heermanni swarthi (Grinnell) (Carrizo Plain Kangaroo Rat)	Dipodomys heermanni swarthi (Grinnell)
Dipodomys heermanni tularensis (C. H. Merriam) (Tulare Kangaroo Rat)	Dipodomys heermanni tularensis (C. H. Merriam)
Dipodomys ingens (C. H. Merriam) (Giant Kangaroo Rat)	Dipodomys ingens (C. H. Merriam)
	Dipodomys nitratooides nitratooides C. H. Merriam (Tipton Kangaroo Rat)
	Dipodomys nitratooides brevinasus Grinnell (Short-nosed Kangaroo Rat)
CASTORIDÆ	
	Castor canadensis subauratus Taylor (Golden Beaver)

* Faunal list from Grinnell (1933).

TABLE 1—Recent mammalian fauna of the McKittrick area*—Continued

Temblor Range	San Joaquin Valley
CRICETIDÆ	
Onychomys torridus tularensis C. H. Merriam (Tulare Grasshopper Mouse)	Onychomys torridus tularensis C. H. Merriam
Reithrodontomys megalotis longicaudus (Baird) (Long-tailed Harvest Mouse)	Reithrodontomys megalotis longicaudus (Baird)
Peromyscus californicus californicus (Gambel) (Parasitic White-footed Mouse)	Peromyscus californicus californicus (Gambel)
Peromyscus maniculatus gambelii (Baird) (Gambel White-footed Mouse)	Peromyscus maniculatus gambelii (Baird)
Peromyscus boyleii rowleyi (Allen) (Rowley White-footed Mouse)	Peromyscus boyleii rowleyi (Allen)
Neotoma lepida gilva Rhoades (Banning Wood Rat)	Neotoma lepida gilva Rhoades
Neotoma fuscipes simplex True (Tejon Wood Rat)	Neotoma fuscipes simplex True
Microtus californicus kernensis R. Kellogg (Kern River Meadow Mouse)	Microtus californicus æstuarinus R. Kellogg (Tule Meadow Mouse)
	Microtus californicus kernensis R. Kellogg
LEPORIDÆ	
Lepus californicus californicus Gray (Calif. Jack Rabbit)	Lepus californicus californicus Gray
Lepus californicus richardsoni Bachman (San Joaquin Jack Rabbit)	Lepus californicus richardsoni Bachman
Sylvilagus auduboni vallicola Nelson (San Joaquin Cottontail)	Sylvilagus auduboni vallicola Nelson
Sylvilagus bachmani bachmani (Waterhouse) (Calif. Brush Rabbit)	Sylvilagus bachmani bachmani (Waterhouse)
CERVIDÆ	
Cervus nannodes C. H. Merriam (Dwarf Elk)	Cervus nannodes C. H. Merriam
Odocoileus hemionus californicus (Caton) (Calif. Mule Deer)	Odocoileus hemionus californicus (Caton)
ANTILOCAPRIDÆ	
Antilocapra americana americana (Ord) (Prong-horn Antelope)	Antilocapra americana americana (Ord)
BOVIDÆ	
Ovis canadensis nelsoni C. H. Merriam (Desert Bighorn)	

* Faunal list from Grinnell (1933).

As is generally true for the southern California Coast Ranges, both the stratigraphy and structure are complex. Indeed, the structure of the McKittrick-Sunset oilfield is so involved that it is difficult to find two geologists familiar with the area who are agreed as to details. In not a few instances points of major importance are still under debate. In the present discussion only the broader features of the geology are treated for the purpose of determining the principal physical events of late Tertiary and early Quaternary time.

The McKittrick formation since its description by Arnold and Johnson has been subdivided into the Etchegoin and Tulare formations

(Pack, 1920, pp. 44-52). The upper Etchegoin may be early Pleistocene in age, but the consensus of opinion seems to be that these beds belong in the late Pliocene (Merriam, 1915A, pp. 40-43). The lower part of the Tulare is likewise regarded as late Pliocene by many geologists, but the upper part of this formation is usually considered as early Quaternary.

Folding movements have affected the Tulare, and this diastrophism would appear therefore to be an early to middle Pleistocene event.

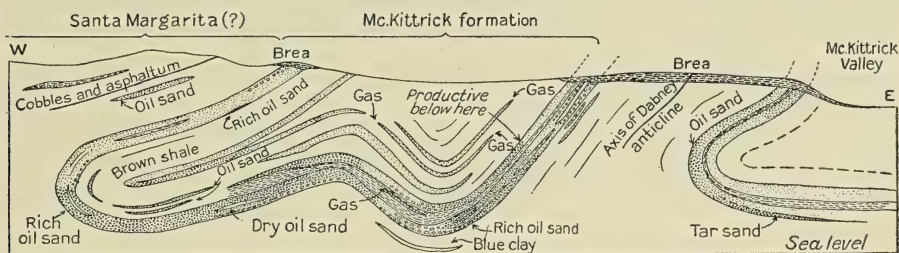


FIG. 2—Generalized structure section of the foothills of the Temblor Range in the vicinity of the fossil occurrence. The Pleistocene vertebrates occur in the brea of McKittrick Valley. Scale 1 inch=approx. 6500 feet. After Arnold and Johnson (1910).

Anderson (1908, pp. 32-35) described a series of upraised Pleistocene terraces in the McKittrick region. These benches extend along much of the southwestern border of the San Joaquin Valley. Their elevation varies from 1200 to 1500 feet above sea-level, or approximately 800 to 1000 feet above the floor of the valley. Their age is difficult to determine precisely, but since at least one of them cuts the Tulare, the period of base-leveling must have extended into the early or middle Pleistocene. Some of the terraces may be older, however.

The fossiliferous brea rests upon one of these terraces with a pronounced unconformity between it and the older beds. The history thus recorded seems to imply an early to middle Quaternary period of folding followed by erosion that resulted in formation of terraces. This was followed by outpouring of tar and renewed uplift. Which of these events occurred first is difficult to determine, and it is possible that they were concomitant. During this period the McKittrick Pleistocene vertebrates were entombed. Consequently, from the geology of the region it would appear that the fauna cannot be older than middle Pleistocene, and it is probable that it is somewhat younger.

OCCURRENCE OF THE MCKITTRICK FAUNA

Oil seeps in various stages of oxidation are not uncommon in the petroleum-producing belt of the southern San Joaquin Valley, and are mentioned or illustrated in nearly all reports on the area. Al-

though vertebrate remains have been reported from the McKittrick area since the time of the Civil War, there is no reliable evidence that any of the earlier finds came from the same horizon as the fauna which forms the basis of this paper.

The seeps in question occupy a narrow zone of some five miles in length just southwest of the village of McKittrick. As is shown by figure 3, the brea belt consists of a more or less continuous zone of local seeps, which in its general northwest trend is parallel to the axis of a major anticline, and it seems quite certain that the oil has found access to the surface along tension cracks in the axis of this

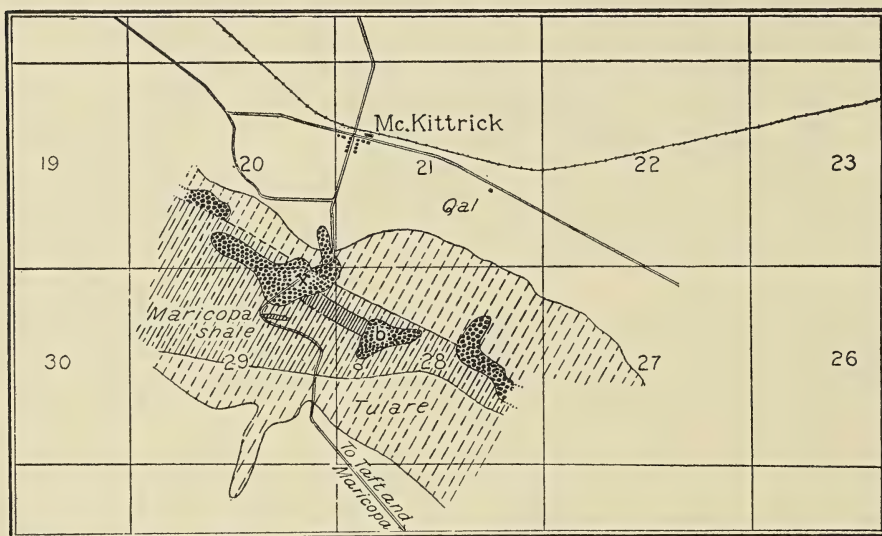


FIG. 3—Geologic map of the McKittrick area, showing relation of the brea seeps (dotted) to underlying formations. Santa Margarita formation indicated by closely spaced diagonal lines. From a previously unpublished map by W. A. English and W. P. Winham.

fold. This conclusion is substantiated by exposures in certain of the gullies cut through the surface layer of hardened petroleum. In these excavations dikes of asphalt, which form the feeders of the surface flows, are exposed.

Most geologists who have studied the area are of the opinion that the original source of the oil is the diatomaceous Maricopa (Monterey) shale, and that at a later time the hydrocarbons migrated into the porous overlying sandstones of the Etchegoin and Tulare formations. In the McKittrick producing district it is generally agreed that the Upper Etchegoin is the principal reservoir rock. Since the anticline which forms the structural trap seems to be in the main post-Tulare in age, the history of the flows may be outlined as follows:

Either contemporaneously with or slightly later than the folding which arched the Tertiary and early Quaternary sediments, oil mi-

grated from the underlying shale into the porous overlying sediments. Contemporaneously with the folding tension cracks formed along the crest of the anticline, and it was along these fissures that the oil reached the surface. From the existing distribution of the seeps, it seems probable that none of the fissures is very extensive laterally, and that the almost continuous belt of brea is actually due to coalescence of numerous individual seeps of slightly different ages rather than to one large flow. V. L. Vander Hoof has informed the writer that during his many visits to the area, he has observed that old seeps often become active after an unknown period of quiescence. It seems reasonable to assume that such was also the case from the earliest inception of the fissures, so that the brea belt rather than constituting one definite horizon actually may represent a complicated sequence of events extending from middle to late Pleistocene time down into the present.

During late Pleistocene time sedimentation was active in the area, and as the oil reached the surface and spread out in sheets of a fraction of an inch or so in thickness it became intercalated with clay, sand, gravel, and wind-blown material. The resulting product is a rudely stratified material consisting of fine and coarse sediments more or less uniformly saturated with petroleum. The upper layers which contain a Recent vertebrate fauna seem to be somewhat better stratified than the lower levels which contain the Pleistocene vertebrates. Vander Hoof (1934) has interpreted stratification of the brea deposit as a form of varves. As is mentioned on page 120 of this paper, this author contends that it was mainly during the summer months that the oil became fluid enough to spread over large areas; while the winter rains carried in most of the clastic material. This conclusion may well be correct, although correlation with other areas, or even between isolated exposures within the same area, seems to be a difficult matter.

From the above it will be seen that while the McKittrick assemblage is often spoken of as a tar pit fauna, conditions of accumulation must have been quite different from those at Rancho La Brea. At the Los Angeles locality deep pools of liquid oil seem to have existed at the surface (Stoner, 1913, p. 392), and these were responsible not only for preservation of fossil remains, but for entrapment of the creatures as well. At the McKittrick locality it seems improbable that the seeps could have had much effectiveness as traps; the principal function of the oil seems to have been as a preservative. As will be seen on a later page, this inference is fully substantiated by the constituency of the fossil fauna.

Vertebrate remains are found at several localities in the McKittrick oil seeps, although all but one, which is located on either side of the

Taft-McKittrick highway, seem to be Recent or sub-Recent accumulations. The Pleistocene deposit is situated in the N.E. $\frac{1}{4}$, N.E. $\frac{1}{4}$ of section 29, T. 30 S., R. 22 E. measured from the Mount Diablo base line and meridian. The locality on the northeast side of the road is known as the University of California locality 4096; while that to the southwest is University of California locality 7139. Locality 138 of the California Institute of Technology comprises essentially the same area as U. C. locality 7139.

At this locality the seeps range upward of ten feet in thickness and rest upon the Santa Margarita and McKittrick formations. Approximately one mile to the northwest an extension of the same flows overlies the alluvium of McKittrick valley. As is shown by Plate 1 the upper surface is irregular, but there seems to be very little evidence of erosion of the petroliferous material since it was laid down. The lower surface is likewise rather irregular, and numerous shallow pipes or depressions which are filled with brea were found to extend down into the underlying sediments. One of the larger of these pipes is shown by Plate 1, fig. 2, and in all cases as this illustration demonstrates, the pockets narrow toward the bottom. The diameter varies from a few inches to several feet. Sternberg (1932, pp. 244-245) records a depth of seventeen feet for one of these peculiar features. In these pockets numerous rodent remains were found, and occasionally larger animals as well. The origin of these pockets is a matter of doubt, but it seems reasonable that some of the smaller pipes may be tar-filled rodent burrows; while the larger openings may represent ancient pot holes subsequently filled with asphalt. This conjecture is supported by other features of the occurrence, for from the greater than average thickness of the tar bands at this locality and the uncommon thickness of the brea itself, it appears that the fossil locality may have been the site of a rather broad and shallow stream valley. In any event, the pipes seen in the McKittrick brea bear only a superficial resemblance to the pits of Rancho La Brea. In the case of the former the pockets definitely terminate in a clay layer, while in the latter instance, the bottom has never been reached by quarrying operations. At McKittrick the oil seems to have seeped down into the pockets, while at Rancho La Brea the pipes represent the fissures along which the petroleum seems to have risen to the surface.

On the upper surface of the brea, dense accumulations of Recent animal bones formed a layer a few inches to a few feet in thickness. Below this layer the Pleistocene fauna was found in considerable abundance. Carnivores and herbivores were mixed indiscriminately throughout the mass, and while most of the skeletons were dismembered, articulated remains and a few almost complete skeletons were found.

The brea does not photograph well, and Plate 1 gives only a vague impression of the enclosing material. In detail the sediments consist of interstratified sand and asphalt. These materials enclose irregularly shaped pockets and lenses of almost pure clay which are almost entirely free from oil. Organic remains are most abundant in the asphaltic material, but to some extent are found in all types of sediment. It is difficult to interpret such intricate sedimentary structures as these, but only two explanations seem plausible. As mentioned above, the locality may mark the site of an old stream valley, in which case interfingering of clay, coarse clastics, and asphalt is due to cut and fill of the stream, which may have operated in conjunction with intermittent outpouring of petroleum. On the other hand, the fossil avian fauna indicates that the locality was also near the shore of a body of standing water. Repeated advance and recession of the shore line might also produce the effects observed. A combination of both conditions is not inconceivable.

During excavation care was taken to separate the obviously Recent material found in the upper layers from the underlying fossil material. It might also have been possible to zone the fossils according to stratigraphic level. This, however, was not attempted, and it cannot be said with assurance that all of the Recent and sub-Recent material was separated from the Pleistocene accumulation. This is especially true for the smaller mammals. However, there seems to be no good reason for assuming that the collections now at hand represent more than a fraction of Pleistocene time, although it is probable that the time span represented by them is somewhat longer than a single glacial or interglacial epoch.

At present the fossil locality is approximately 1000 feet above sea-level, or nearly 700 feet above the level of Buena Vista Lake. Furthermore, if the existing topography corresponds even roughly to that of the late Pleistocene, it would not be possible for heavier rainfall alone to have brought into existence a lake at this elevation. Such a body of water would flood most of the San Joaquin Valley, and there is no evidence of a lake of such dimensions. According to Blake (1856), "the greater part of Tulare Valley was formerly submerged by a broad lake." This water body could hardly have extended into the McKittrick area, and there is no reason for assuming that it was a remnant of a Pleistocene lake. Consequently, it seems necessary to conclude that the ancient lake at McKittrick had some physiographic or structural cause. Since it is known that the region is still tectonically active, it does not seem unreasonable to infer that uplift and erosion subsequent to fossil accumulation brought about extinction of the lake. This inference has an important bearing upon interpretation of the fossil assemblage and will be developed more fully on a later page.

In review then, the McKittrick breia forms a definitely stratified layer which rests with unconformity upon folded Tertiary and early Pleistocene sediments. No continuously baited traps such as those which existed at Rancho La Brea seem to have been present at McKittrick, and this appears to have been an important factor in bringing about some of the faunal features in which the latter occurrence contrasts with the former.

PRESERVATION OF FOSSIL REMAINS

As in the case of Rancho La Brea, the McKittrick fossils are thoroughly saturated with bitumen, which has penetrated into sinuses of skulls and into the marrow cavities of the long bones. Aside from the dark-brown to black color imparted by the bitumen, the osseous material has remained unchanged. All skull openings are filled with sand and tar, which has carried into these cavities the remains of rodents and other small mammals. Surface markings which show the courses of nerves and blood vessels are occasionally preserved. Pit wear (Stock, 1930, p. 27) and tooth marks of rodents (Stock, 1929), so often seen on bones from Rancho La Brea, are rarely encountered on specimens from McKittrick. Absence of pit wear is perhaps explained by the surficial nature of the McKittrick tar seeps, which may have prevented differential motion of the matrix; while presence of large bodies of standing water may have prevented incursion of rodents.

An interesting difference in state of preservation of the McKittrick and Rancho La Brea bones has been brought to the writer's attention by V. L. Vander Hoof. In bones from Rancho La Brea nearly all lacunæ are completely filled with tar; while in osseous material from McKittrick these canals often are either entirely free from hydrocarbons or only partially saturated by this substance. Whether less thorough saturation of the McKittrick bones is to be attributed to their more recent burial, or to some unknown difference in character of the oils, remains an open question.

Two types of staining are observed: one of an intensely black color and almost vitreous lustre, the other of a light to dark-brown shade and wax-like appearance. Nearly all rodents and lagomorphs from McKittrick show the first type of appearance; while the second type is usually exhibited by remains of larger mammals. Since the rodents and lagomorphs were in the main collected from somewhat higher levels than the larger forms, it suggests that the first type of appearance indicates a relatively recent age for the small mammals. As indicated on pages 135-140, there are other reasons for believing that a part of the McKittrick rodent and lagomorph assemblages is Recent or sub-Recent in age.

Compared with Rancho La Brea nearly all mammalian material from McKittrick is poorly preserved. Perfect skulls are rare, and articulated elements are seldom found. This is to be attributed perhaps to the character of the McKittrick seeps. Apparently only in rare instances were animals actually engulfed by the tar. In a majority of cases preservation may have depended upon chance contact of petroleum with osseous material. Consequently, considerable decay may have occurred prior to its saturation by the hydrocarbons.

The relatively poor state of preservation of mammalian remains is in marked contrast to the very perfect preservation of the avifauna. According to Miller (1925, p. 308) the McKittrick birds are better preserved than those of Rancho La Brea. To quote from this author:

"The matrix and immediate entombment are not seen to differ in any degree from these same factors at Rancho La Brea. . . . Furthermore, the factor of weathering was largely eliminated, so that specimens not broken by differential motion in the matrix have the most minute characters of the bone beautifully preserved. For some reason not clearly evident, the specimens are more fragile than those from Rancho La Brea. A difference in composition of the oil is presumed to be the factor responsible, since the matrix appears more friable and of lighter brown color than the darker, more tenacious asphalt of Rancho La Brea."

Why bird remains from McKittrick should be better preserved than those of the mammals is not clearly evident. Perhaps such relatively small forms as birds were completely covered by the limited amount of asphalt available at any one time, while with larger forms this was not possible.

The percentage of old, young, and diseased animals in the McKittrick fauna does not appear to be higher than normal. This is in marked contrast to Rancho La Brea, where an exceptionally high proportion of such types is found (Merriam, 1911, pp. 209-210). Here again the supposition that the McKittrick seeps did not function as traps to so great an extent as those of Rancho La Brea seems to be borne out.

FOSSIL FAUNAS OF MCKITTRICK AND RANCHO LA BREA

Table 2 lists the mammals now known from McKittrick and Rancho La Brea, while table 3 lists the birds. No tabulation of the faunas from the Carpinteria and Palos Verdes beds is made, but of the twenty-seven species of mammals known from the former locality nearly all of the genera and many of the species occur also at Rancho La Brea. The fifteen mammalian forms found in the Upper San Pedro, or Palos Verdes beds, are all found at Rancho La Brea, and

as Stock (1925, pp. 118-119) has indicated furnish some basis for correlation of the two deposits.

TABLE 2—*Fossil mammalian faunas of McKittrick and Rancho La Brea*

McKittrick	Rancho La Brea
FELIDÆ	
Smilodon californicus Bovard	Smilodon californicus Bovard Smilodon californicus brevipes Merriam and Stock
Felis atrox Leidy	Felis ** atrox Leidy * Felis bituminosa Merriam and Stock
Felis daggetti Merriam	Felis concolor Linnæus Felis daggetti Merriam
Lynx rufa fischeri Merriam	Lynx * rufa fischeri Merriam
CANIDÆ	
Canis latrans orcutti Merriam	Canis * latrans orcutti Merriam Canis andersoni Merriam Canis occidentalis furlongi Merriam
Ænocyon dirus (Leidy)	Ænocyon ** dirus (Leidy) *
Ænocyon near milleri (Merriam)	Ænocyon milleri (Merriam)
Vulpes macrotis cf. mutica C. H. Merriam	Urocyon * californicus (Mearns)
MUSTELIDÆ	
Mustela frenata nigriauris Hall	Mustela frenata latirostra Hall *
Mephitis mephitis holzneri Mearns	Mephitis mephitis holzneri Mearns *
Spilogale phenax phenax C. H. Merriam	Spilogale phenax microrhina Hall *
Taxidea taxus cf. neglecta Mearns	Taxidea taxus cf. neglecta Mearns *
URSIDÆ	
Tremarctotherium simum (Cope)	Tremarctotherium simum (Cope)
Ursus optimus n. sp.	Ursus optimus n. sp.
MEGATHERIIDÆ	
Megalonyx? sp.	Megalonyx ** jeffersoni californicus Stock Nothrotherium shastense Sinclair
MYLODONTIDÆ	
Paramylodon harlani (Owen)	Paramylodon harlani (Owen) Paramylodon harlani tenuiceps (Stock)
CAMELIDÆ	
Camelops hesternus (Leidy)	Camelops hesternus (Leidy) * **
Tanupolama stevensi (Merriam and Stock)	
EQUIDÆ	
Equus occidentalis Leidy	Equus occidentalis Leidy *
BOVIDÆ	
Preptoceras? cf. sinclairi Furlong	
Bison antiquus Leidy	Bison * ** antiquus Leidy
CERVIDÆ	
Cervus sp.	
Odocoileus sp.	Odocoileus sp. indet. * **
ANTILOCAPRIDÆ	
Capromeryx minor Taylor	Capromeryx minor Taylor **
Antilocapra americana (Ord)	Antilocapra americana (Ord)

* Indicates that the form is found at Carpinteria.

** Indicates that the form is found in the Upper San Pedro (Palos Verdes beds).

TABLE 2—*Fossil mammalian faunas of McKittrick and Rancho La Brea—Continued*

McKittrick	Rancho La Brea
ELEPHANTIDÆ	
Parelephas columbi (Falconer)	Parelephas columbi (Falconer) Archidiskodon imperator (Leidy)*
MASTODONTIDÆ	
Mastodon raki Frick	Mastodon americanus (Kerr)
TAYASSUIDÆ	
Platygonus near compressus Le Conte	Platygonus sp.
TAPIRIDÆ	
	Tapirus? sp.
SCIURIDÆ	
Otospermophilus cf. grammurus (Say)	Otospermophilus grammurus (Say)
Ammospermophilus cf. nelsoni (C. H. Merriam)	
GEOMYIDÆ	
Thomomys bottæ bottæ (Eydoux and Gervais)	Thomomys bottæ*** occipitalis Dice
HETEROMYIDÆ	
Dipodomys near ingens (C. H. Merriam)	Dipodomys* agilis Gambel
Perognathus cf. inornatus C. H. Merriam	Perognathus* californicus C. H. Merriam
CRICETIDÆ	
Onychomys? sp.	Onychomys* torridus ramona Rhoades
Reithrodontomys? sp.	Reithrodontomys megalotis longicaudus (Baird)
Peromyscus cf. californicus (Gambel)	Peromyscus* imperfectus Dice
Neotoma lepida gilva Rhoades	Neotoma*** sp. indet.
Microtus californicus æstuarinus R. Kellogg	Microtus californicus neglectus L. Kellogg
	Microtus californicus (Peale)***
LEPORIDÆ	
Lepus californicus Gray	Lepus* californicus Gray
Sylvilagus bachmani (Waterhouse)	Sylvilagus bachmani cinerascens (Allen)
Sylvilagus auduboni (Baird)	Sylvilagus*** auduboni pix Dice
SORICIDÆ	
Sorex cf. ornatus (C. H. Merriam)	Sorex cf. ornatus (C. H. Merriam)*
	Notiosorex crawfordi Coues
VESPERTILIONIDÆ	
Antrozous pallidus pacificus C. H. Merriam	

* Indicates that the form is found at Carpinteria.

** Indicates that the form is found in the Upper San Pedro (Palos Verdes beds).

Comparison of tables 1 and 2 reveals that many of the forms found fossil in the McKittrick tar seeps are still living in the area, as is especially true in case of the rodents. Indeed, the rodent fauna is so similar to that still living in the area as to suggest that it may be in

TABLE 3—*Fossil avian faunas of McKittrick and Rancho La Brea*

McKittrick	Rancho La Brea
COLYMBIDÆ—Grebes	
Podilymbus podiceps (Linnæus)	Colymbus sp. indet. (Grebe) Podilymbus podiceps (Linnæus) (Pied-billed Grebe)
ARDEIDÆ—Hérons and Bitterns	
Ardea herodias Linnæus	Ardea herodias Linnæus (Great Blue Heron) Casmerodius albus (Gmelin) (American Egret) Egretta thula? (Molina) (Snowy Egret) Florida cærulea? (Linnæus) (Little Blue Heron) Butorides virescens (Linnæus) (Green Heron)
Nycticorax nycticorax (Linnæus)	Nycticorax nycticorax (Linnæus) (Night Heron) Botaurus lentiginosus (Montagu) (American Bittern)
CICONIIDÆ—Storks and Wood Ibises	
Ciconia † maltha Miller	Mycteria americana Linnæus (Wood Ibis) Mycteria † wetmorei Howard (La Brea Wood Ibis) Ciconia † maltha Miller * (Brea Stork)
THRESKIORNITHIDÆ—Ibises and Spoonbills	
Ajaia ajaja (Linnæus)	Plegadis guarauna (Linnæus) (White-faced Glossy Ibis) Ajaia ajaja (Linnæus)? (Roseate Spoonbill)
ANATIDÆ—Swans, Geese, and Ducks	
Cygnus columbianus (Ord)	Cygnus columbianus (Ord) (Whistling Swan)
Branta canadensis (Linnæus)	Branta canadensis (Linnæus) ** (Canada Goose)
Branta † dickeyi Miller (Giant Goose)	Branta sp. indet. Anser albifrons (Scopoli) ** (White-fronted Goose) Chen hyperborea (Pallas) (Lesser Snow Goose) Chen rossi? (Cassin) (Ross's Goose)
Anabernicula ‡ minuscula (Wetmore)	Anabernicula ‡ minuscula (Wetmore) (Pigmy Goose)
Anas platyrhynchos Linnæus	Anas platyrhynchos Linnæus * ** (Common Mallard)
Chaulelasmus streperus (Linnæus)	Chaulelasmus streperus (Linnæus) (Gadwall)
Mareca americana (Gmelin) (Baldpate)	Nettion carolinense (Gmelin) ** (Green-winged Teal)
Dafila acuta? (Linnæus) (Pintail Duck)	Querquedula sp. indet.
Nettion carolinense (Gmelin)	
Querquedula cyanoptera (Vieillot) ** (Cinnamon Teal)	
Spatula clypeata (Linnæus)	Spatula clypeata? (Linnæus) (Shoveller Duck)

* Indicates that the form is also present at Carpinteria.

** Indicates that the form is also present in the Palos Verdes (Upper San Pedro beds).

‡ Indicates that the genus is extinct.

† Indicates that the species is extinct.

TABLE 3—*Fossil avian faunas of McKittrick and Rancho La Brea—Continued*

McKittrick	Rancho La Brea
ANATIDÆ—Swans, Geese, and Ducks— <i>Continued</i>	
	Nyroca valisineria? (Wilson) (Canvas-back Duck)
Nyroca affinis? (Eyton) (Lesser Scaup Duck)	
Nyroca americana (Eyton) (Red-head Duck)	
Charitonetta albeola (Linnæus) (Buffle-head Duck)	
Erismatura jamaicensis (Gmelin) (Ruddy Duck)	
CATHARTIDÆ—American Vultures	
Cathartes aura (Linnæus)	Cathartes aura (Linnæus)* ** (Turkey Vulture)
Coragyps † occidentalis (Miller)	Coragyps † occidentalis (Miller)* (Black Vulture)
	Gymnogyps californianus (Shaw)* (California Condor)
	Vultur † clarki (Miller) (Vulture)
	Cathartornis ‡ gracilis Miller (Vulture)
TERATORNITHIDÆ—Teratornithes	
Teratornis ‡ merriami Miller	Teratornis ‡ merriami Miller * (Teratornithes)
ACCIPITRIDÆ—Kites, Hawks, and Allies	
	Elanus leucurus (Vieillot) (White-tailed Kite)
	Astur atricapillus (Wilson)* (Goshawk)
	Accipiter velox (Wilson)* (Sharp-shinned Hawk)
Accipiter cooperi (Bonaparte)	Accipiter cooperi (Bonaparte) (Cooper's Hawk)
	Buteo sp. indet.*
Buteo borealis (Gmelin)	Buteo borealis (Gmelin)* (Red-tailed Hawk)
Buteo swainsoni Bonaparte	Buteo swainsoni Bonaparte (Swainson's Hawk)
	Buteo lagopus (Gmelin) (American Rough-legged Hawk)
Buteo regalis (Gray)	Buteo regalis (Gray) (Ferruginous Rough-leg)
Urubitinga † fragilis (Miller)	Urubitinga † fragilis (Miller)* (Fragile Eagle)
Aquila chrysaëtos (Linnæus)	Aquila chrysaëtos (Linnæus)* (Golden Eagle)
Haliaeetus leucocephalus Linnæus	Haliaeetus leucocephalus Linnæus (Bald Eagle)
Neogyps ‡ errans Miller	Neogyps ‡ errans Miller * (Errant Eagle)
Neophrontops ‡ americanus Miller	Neophrontops ‡ americanus Miller (American Neophron)
	Morphnus † woodwardi Miller (Woodward Eagle)
	Wetmoregyps ‡ daggetti (Miller) (Daggett Eagle)
	Spizaëtus † grinnelli (Miller)* (Grinnell Eagle)
Circus hudsonius (Linnæus)	Circus hudsonius (Linnæus)* (Marsh Hawk)

* Indicates that the form is also present at Carpinteria.

** Indicates that the form is also present in the Palos Verdes (Upper San Pedro beds).

‡ Indicates that the genus is extinct.

† Indicates that the species is extinct.

TABLE 3—*Fossil avian faunas of McKittrick and Rancho La Brea*—Continued

McKittrick	Rancho La Brea
FALCONIDÆ—Caracaras and Falcons	
Polyborus cheriway (Jacquin)	Polyborus cheriway (Jacquin)* (Audubon's Caracara)
Falco mexicanus Schlegel	Falco mexicanus Schlegel (Prairie Falcon)
Falco peregrinus Tunstall	Falco peregrinus Tunstall (Peregrine Falcon)
Falco columbarius Linnæus	Falco columbarius Linnæus (Pigeon Hawk)
Falco sparverius Linnæus	Falco sparverius Linnæus* (Sparrow Hawk)
Falco † swarthi Miller (Giant Falcon)	
Falco sp. indet.	Falco sp. indet.
PERDICIDÆ—Partridges and Quails	
Lophortyx californica (Shaw)	Lophortyx californica? (Shaw)** (California Quail)
MELEAGRIDIDÆ—Turkeys	
	Parapavo ‡ californicus Miller* (California Turkey)
GRUIDÆ—Cranes	
Grus canadensis (Linnæus)	Grus canadensis (Linnæus) (Little Brown Crane)
	Grus americana? (Linnæus) (Whooping Crane)
RALLIDÆ—Rails, Gallinules, and Coots	
Rallus limicola Vieillot (Virginia Rail)	Fulica americana Gmelin (American Coot)
CHARADRIIDÆ—Plovers, Turnstones, and Surf-Birds	
Eupoda montana (Townsend) (Mountain Plover)	
Oxyechus vociferus (Linnæus)	Oxyechus vociferus (Linnæus) (Killdeer)
	Squatarola squatarola (Linnæus) (Black-bellied Plover)
SCOLOPACIDÆ—Woodcock, Snipe, and Sandpipers	
Numenius americanus Beckstein	Capella delicata (Ord) (Wilson's Snipe)
	Numenius americanus Beckstein (Long-billed Curlew)
	Phæopus hudsonicus (Latham) (Hudsonian Curlew)
Totanus melanoleucus (Gmelin)	Totanus melanoleucus (Gmelin) (Greater Yellow-legs)
Pelidna alpina (Linnæus) (Dunlin)	
Limnodromus griseus (Gmelin)	Limnodromus griseus (Gmelin) (Dowitcher)
	Limosa fedoa? (Linnæus) (Marbled Godwit)
RECURVIROSTRIDÆ—Avocets and Stilts	
Recurvirostra americana Gmelin	Recurvirostra americana Gmelin (Avocet)

* Indicates that the form is also present at Carpinteria.

** Indicates that the form is also present in the Palos Verdes (Upper San Pedro beds).

‡ Indicates that the genus is extinct.

† Indicates that the species is extinct.

TABLE 3—*Fossil avian faunas of McKittrick and Rancho La Brea—Continued*

McKittrick	Rancho La Brea
LARIDÆ—Gulls and Terns	
	Larus brachyrhynchus? Richardson (Short-billed Gull)
	Rissa tridactyla? (Linnæus) (Kittiwake)
COLUMBIDÆ—Pigeons and Doves	
	Columba fasciata Say * (Bend-tailed Pigeon)
Zenaidura macroura (Linnæus)	Zenaidura macroura carolinensis (Linnæus) (Mourning Dove)
	Ectopistes migratorius (Linnæus) (Passenger Pigeon)
CUCULIDÆ—Cuckoos, Roadrunners, and Anis	
Geococcyx californianus (Lesson)	Geococcyx californianus * (Lesson) (Roadrunner)
TYTONIDÆ—Barn Owls	
	Tyto alba (Scopoli) * (Barn Owl)
STRIGIDÆ—Typical Owls	
	Otus asio (Linnæus) * (Screech Owl)
Bubo virginianus (Gmelin)	Bubo virginianus (Gmelin) * (Great Horned Owl)
	Glaucidium gnoma Wagler (Pigmy Owl)
Speotyto cunicularia (Molina)	Speotyto cunicularia (Molina) (Burrowing Owl)
	Strix † brea Howard (La Brea Owl)
Asio wilsonianus (Lesson)	Asio wilsonianus (Lesson) * (Long-eared Owl)
	Asio flammeus (Pontoppidian) (Short-eared Owl)
	Cryptoglaux acadica (Gmelin) (Saw-whet Owl)
PICIDÆ—Woodpeckers	
Colaptes cafer (Gmelin)	Colaptes cafer (Gmelin) * (Flicker)
	Asyndesmus lewis Gray (Lewis's Woodpecker)
TYRANNIDÆ—Tyrant Flycatchers	
	Tyrannus sp. (Kingbird)
ALAUDIDÆ—Larks	
	Octocoris alpestris (Linnæus) (Horned Lark)
HIRUNDINIDÆ—Swallows	
Petrochelidon albifrons (Rafinesque) (Cliff Swallow)	
CORVIDÆ—Jays, Magpies, and Crows	
	Aphelocoma * sp. (Jay)
	Pica nuttalli (Audubon) * (Yellow-billed Magpie)
Corvus corax Linnæus	Corvus corax Linnæus * (Raven)
	Corvus brachyrhynchus Brehm (Crow)
	Corvus caurinus Baird * (Northwest Crow)

* Indicates that the form is also present at Carpinteria.

† Indicates that the species is extinct.

TABLE 3—*Fossil avian faunas of McKittrick and Rancho La Brea—Continued*

McKittrick	Rancho La Brea
PARIDÆ—Titmice, Verdins, and Bush-Tits	
	Penthestes sp.* (Chickadee)
MIMIDÆ—Mockingbirds and Thrashers	
	Toxostoma cf. redivivum (Gambel) (California Thrasher)
BOMBYCILLIDÆ—Waxwings	
	Bombycilla cedrorum Vieillot * (Cedar Waxwing)
LANIIDÆ—Shrikes	
	Lanius ludovicianus Linnaeus (Loggerhead Shrike)
ICTERIDÆ—Meadowlarks, Blackbirds, and Troupials	
	Sturnella neglecta? Audubon *** (Western Meadowlark)
	Xanthocephalus? sp. (Yellow-headed Blackbird)
	Icterus sp. (Oriole)
	Euphagus † magnirostris A. H. Miller (La Brea Blackbird)
	Agelaius phoeniceus californicus Nelson (Bicolored Red-wing)
FRINGILLIDÆ—Grosbeaks, Finches, Sparrows, and Buntings	
	Pipilo * sp. indet. (Towhee)

* Indicates that the form is also present at Carpinteria.

** Indicates that the form is also present in the Palos Verdes (Upper San Pedro beds).

† Indicates that the species is extinct.

part post-Pleistocene in age. Furthermore, in the fossil assemblage plains-dwellers apparently greatly outnumber mountain-living forms.

In the case of extinct forms, the habitat cannot be determined definitely; but it would appear that at McKittrick mountain-dwellers are relatively somewhat more abundant than at Rancho La Brea. Owing to closer proximity of the former locality to uplands, this is perhaps not surprising. It would seem therefore, that the McKittrick fossil assemblage affords a valuable transitional stage between the predominantly plains assemblage of Rancho La Brea and the upland faunas of the northern California caves.

Forms which occur as fossils at either McKittrick or Rancho La Brea, and which may have been mountain-dwellers are: *Lynx rufa fischeri*, *Felis daggetti*, *Mustela frenata nigriauris*, *Tremarctotherium simum*, *Ursus optimus*, *Tanupolama stevensi*, and *Preptoceras? sinclairi*.

Among the larger mammals only four species, *Vulpes macrotis*, *Antilocapra americana*, *Odocoileus*, and *Cervus*, which inhabit the McKittrick area at the present time are found in the tar pits. Specific

identification of the deer and elk is very uncertain, but there seems to be little difference between the fossil and living forms. Most of the remaining large mammals found in the fossil assemblage are definitely extinct and seem to have left no descendants in the region, although *Ursus optimus* and *Canis latrans orcutti* may be ancestral to living forms.

Examination of table 2 serves to point out the very striking similarity in mammalian faunas of McKittrick and Rancho La Brea. Some noteworthy differences are likewise apparent. Of the latter, perhaps the most striking is the absence of *Preptoceras?* and *Tanupolama* at Rancho La Brea. In view of the unusual number of individuals known from this locality, it seems very probable that these forms did not live in the Los Angeles area at a time when the fossil assemblage was accumulating. This problem is discussed more fully below.

Of the 43 species of mammals occurring at McKittrick 20 are no longer living, while of the 49 species found at Rancho La Brea 29 are extinct. It would appear, furthermore, that extinction at Rancho La Brea has been confined largely to larger forms, for only one rodent species, *Peromyscus imperfectus*, and three of the subspecies seem to be extinct. In the McKittrick rodent assemblage, apparently, all of the species are still living, although one, *Thomomys bottæ bottæ*, seems to live no longer in the region. While the McKittrick rodents may be partly Recent in age, it seems probable that members of this order have not been affected by extinction to so great an extent as the larger mammalian forms. This presumption has considerable bearing upon accuracy of the percentage method of correlation. Most Pleistocene faunas are relatively poor in representation of the rodents; consequently, indiscriminate methods of calculation which do not take into consideration differences in life spans of the smaller and larger mammals can hardly be convincing.

Of the 105 species of fossil birds now known from Rancho La Brea, sixteen are extinct. Fifty-eight species of birds are known from McKittrick. Of these nine are known to be no longer living. The percentage of extinct forms would thus appear to be approximately fifteen and one-half in both instances. As Miller (1925, p. 311) has noted, migratory species are relatively somewhat more abundant at McKittrick, and since such forms may be expected to have a better chance of survival, no definite statement of relative age of the two deposits can be made on the basis of avifaunas alone. The percentage of extinct mammals at McKittrick is approximately 46 as compared with 59 at Rancho La Brea. On this basis it might appear that McKittrick is somewhat younger than Rancho La Brea. The writer must confess, however, that whenever doubt has arisen as to whether a given

mammalian form is to be referred to an extinct or living species, he has always favored the latter interpretation. In view of the relatively small percentage differences between the two faunas, not much reliance is to be placed upon these figures as indicators of relative age. As shown on pages 155-156, however, there are other and better reasons for believing McKittrick to be a little younger than Rancho La Brea.

The only birds found at Carpinteria which do not also occur at McKittrick or Rancho La Brea are: *Buteo lineatus* (Gmelin) (Red-shouldered Hawk), *Dryobates* sp. (Woodpecker), *Sayornis* sp. (Phoebe-Flycatcher), *Empidonax* sp. (Small Flycatcher), *Cyanocitta stelleri* (Gmelin) (Steller's Jay), *Sitta canadensis* Linnæus (Red-breasted Nuthatch), *Chamæa fasciata* (Gambel) (Wren-tit), *Turdus migratorius* Linnæus (Robin), *Hylocichla*? sp. (Thrush), *Spinus pinus* (Wilson) (Pine Siskin), *Loxia curvirostra* Linnæus (Red Crossbill), and *Passerella iliaca* (Merrem) (Fox Sparrow). All are still living. Many of the above are woodland forms, and their absence at McKittrick and Rancho La Brea is readily explained by lack of adequate forest cover in the vicinity of the tar deposits.

Birds found in the Palos Verdes beds, but which have not yet been encountered in asphalt deposits, are: *Gavia near immer* (Bruennich) (Loon), *Synthliboramphus antiquus* (Gmelin) (Ancient Murrelet), *Diomedea near nigripes* Audubon (Black-footed Albatross), *Puffinus opisthomelas* Coues (Black-vented Shearwater), *Fulmarus glacialis* (Linnæus) (Fulmer), *Phalacrocorax penicillatus* (Brandt) (Cormorant), and *Oidemia perspicillata* (Linnæus) (Surf Scoter). All these species are still in existence. In this instance it seems reasonable to attribute dissimilarities between the avifauna and those of the tar pits to proximity of the ocean and lack of woods at the San Pedro locality.

Examination of table 3 reveals that twelve species of birds found at McKittrick do not occur at Rancho La Brea. Of these, seven are aquatic or semi-aquatic in habit. Thus the major differences may be accounted for by absence of large bodies of standing water at the Los Angeles locality. Fifty-nine species of birds occurring at Rancho La Brea are not found at McKittrick. Reasons for absence of some of these forms from the San Joaquin Valley locality will be discussed on a later page. In this connection it should be kept in mind that the McKittrick passerines have not yet been thoroughly studied.

Since birds are perhaps somewhat longer lived than mammalian species, it is not surprising that insofar as avian faunas are concerned, there seems to be little reason for regarding the McKittrick, Rancho La Brea, Carpinteria, and Palos Verdes assemblages as other than closely related in time.

FOSSIL FLORAS OF MCKITTRICK, RANCHO LA BREA,
AND CARPINTERIA

In order to complete the extraordinary picture of late Pleistocene life afforded by the asphalt assemblages, it seems desirable to list the floras. The plant assemblage of Carpinteria is particularly well known. In case of McKittrick and Rancho La Brea it seems reasonably certain that in the immediate vicinity of the tar seeps no woods were present, but it is probable that during the period of fossil accumulation both the Temblor and Santa Monica Ranges were forest-covered.

The Carpinteria floral list has been compiled from Chaney and Mason (1933, p. 52). According to these authors, only one species found at this locality, *Pyrus hoffmanni*, is new. The remainder belongs to the living flora of California, and most of the species are also known from other Pleistocene deposits in the state. The ecologic relations are those of the Monterey pine forest, which at present occurs typically on the Monterey Peninsula, although scattered groves are found as far south as Morro Rock in San Luis Obispo County. Consequently, a northward retreat of the forest seems to have been the only important change in the plant world since the deposit was laid down. Chaney and Mason (1933, pp. 75-76) are of the opinion that the southward extension of the pine forest was brought about by glaciation.

Frost (1927, pp. 85-87) who is the authority for the Rancho La Brea floral list points out that all of the species found at this locality with the exception of *Celtis mississippiensis reticulata* live today in Monterey County. All are elements of the mesophytic forest except *Sambucus glauca*, which is hygrophytic. Present distribution of *C. m. reticulata* is largely confined to mountain ranges bordering deserts, and Frost considers occurrence of this plant at Rancho La Brea as inconsistent with character of the remainder of the flora. He suggests that the seeds of this plant, which constitute its entire record at Rancho La Brea, may well have been carried into the area by birds. The conclusion reached by Frost is that a comparison of the existing climates of the Monterey and Los Angeles areas should serve as an indicator of the climatic change which has occurred since Rancho La Brea time. According to this view, there would appear to be a marked similarity between the floras of Rancho La Brea and Carpinteria.

At a later time Mason (Compton, 1937, p. 88) offered a quite different interpretation of the Rancho La Brea flora. This author points out that the taxonomic aspect of the pine is in doubt; while the cypress could as well be similar to *Cupressus nevadensis* as to *C. goveniana* or *C. macrocarpa*. When reasonable allowance for these

McKittrick	Carpinteria	Rancho La Brea
Juniperus utahensis	Cupressus goveniana (Mountain Cypress)	Cupressus macrocarpa (Monterey Cypress)
Pinus monophylla	Juniperus californica (Juniper)	Juniperus californica *
	Pinus muricata (Pine)	Pinus muricata **
	Pinus radiata (Monterey Pine)	
	Pinus remorata (Santa Cruz Pine)	
	Pinus sabiniana (Digger Pine)	
	Pseudotsuga taxifolia (Douglas Fir)	
	Quercus agrifolia (Live Oak)	Quercus agrifolia
	Sequoia sempervirens (Redwood)	
	Umbellularia californica (Spice Wood)	
Arctostaphylos glauca	Arctostaphylos glauca (Big-berried Manzanita)	
Prunus ilicifolia (California Wild Plum)	Arctostaphylos sp.	
Atriplex sp. (Salty Sage)	Eriodictyon californicum (Yerba Santa)	
	Ceanothus thyrsiflorus (Blue Blossom Lilac)	
	Garrya elliptica (Quinine Bush)	
	Pyrus hoffmanni (Extinct Pear)	
	Rhus diversiloba (Poison Oak)	Celtis mississippiensis reticulata (Western Hackberry)
	Sambucus glauca (Blue Elderberry)	Sambucus glauca
	Arceuthobium campylopodum (Mistletoe)	
	Chorizanthe pungens (Turkish Rugging)	Undetermined Compositæ?
	Corethrogyne sp.	
	Cymopterus littoralis	
	Pteris aquilina (Common Brake)	
	Xanthium calvum (Cocklebur)	

** *P. tuberculata* of Frost

For the floral list of McKittrick I am indebted to Dr. Mason, who states in conversation that this assemblage is likewise of a dry interior aspect. *Juniperus utahensis* and *Atriplex* are somewhat out

of their present range, although the latter occurs abundantly on the lowlands a few miles from the fossil deposit. It is hoped that Mason's report on the McKittrick flora will appear before publication of this paper.

CENSUS OF THE MCKITTRICK FOSSIL MAMMALS

The method employed in estimating relative abundance is essentially the same as that used by Stock (1929A, p. 282) for a census of the Rancho La Brea mammals. However, Stock considered only adult animals, while in this case individuals in all stages of growth are considered. In both instances, however, the count seems to represent some basis for comparison of the two mammalian faunas.

Figures 4 and 5 illustrate relative abundance of individuals of various mammalian orders at McKittrick and Rancho La Brea, while figure 6 contrasts the relative abundance of individuals of various species at the two localities. In all cases rodents, insectivores, and bats have been omitted.

Although the McKittrick collection comprises only 355 individuals as compared with 4264 in the Rancho La Brea collection of the Los Angeles Museum, there seems to be a fair basis for comparison of the two faunas. Perhaps the most important difference in constituency is the comparatively meager representation of carnivores at McKittrick. As is shown by figure 6, the Carnivora of McKittrick are predominantly modernized forms such as the coyote, while at Rancho La Brea types like *Aenocyon* and *Smilodon* comprise the greater part of the carnivore population.

Unfortunately no statistical studies of the smaller mammals of Rancho La Brea have been made. With regard to the lagomorphs, the cottontail, *Sylvilagus auduboni*, seems to be the most abundant at McKittrick and is represented by no less than 54 individuals. The jack rabbit, *Lepus californicus*, is next in order of abundance with 41 individuals, while the brush rabbit, *Sylvilagus bachmani*, numbers approximately 28. Following Wilson's determinations (1933, pp. 63-65), it would appear that representation of the lagomorphs is approximately similar to that at Rancho La Brea, but at Carpinteria *Sylvilagus bachmani* is relatively common while *Lepus* is rare.

At McKittrick representation of the rodents is as follows: *Dipodomys*, 255; *Peromyscus*, 100; *Microtus*, 35; *Thomomys*, 16; *Ammospermophilus*, 9; *Perognathus*, 8; and *Otospermophilus* and *Onychomys* with one individual each. According to Wilson, at Rancho La Brea *Thomomys* is the most abundant rodent; while at Carpinteria *Peromyscus* is the most abundant form. As this author points out,

these facts may have no special significance insofar as environmental conditions are concerned, but the great abundance of *Dipodomys* in the McKittrick fauna suggests an arid to semi-arid climate, for the kangaroo rats characteristically inhabit regions of low rainfall. The evidence of the rodent fauna is apparently in disagreement with the evidence of the birds, and perhaps also with that of the larger mammals, which seem to indicate more humid conditions. In this con-

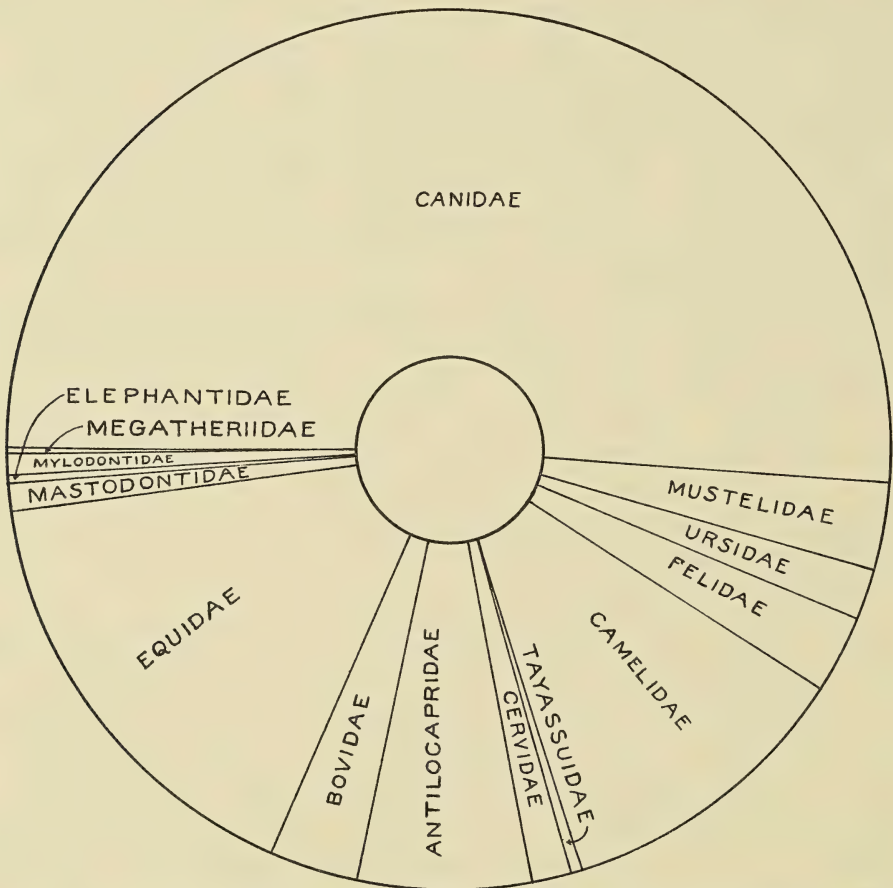


FIG. 4—Diagram showing relative number of individuals in the mammalian families (except rodents, lagomorphs, insectivores, and bats) occurring in the McKittrick Pleistocene fauna.

nection it should be noted how very similar the fossil rodent fauna is to that still inhabiting the area, for only one variety, *Thomomys bottæ bottæ*, seems to live no longer in the region.

Insectivores and bats are not at all abundant at McKittrick, and are represented by not more than one or two individuals each.

CENSUS OF THE McKITTRICK FOSSIL AVIFAUNA

Present knowledge of the McKittrick birds is due almost entirely to the work of L. H. Miller. The collections now reported consist of approximately 4000 specimens. This number although large in comparison with that from other fossil localities, is insignificant when compared with the 86,242 bird bones in the Rancho La Brea collections of the Los Angeles Museum. The passerines of McKittrick have not

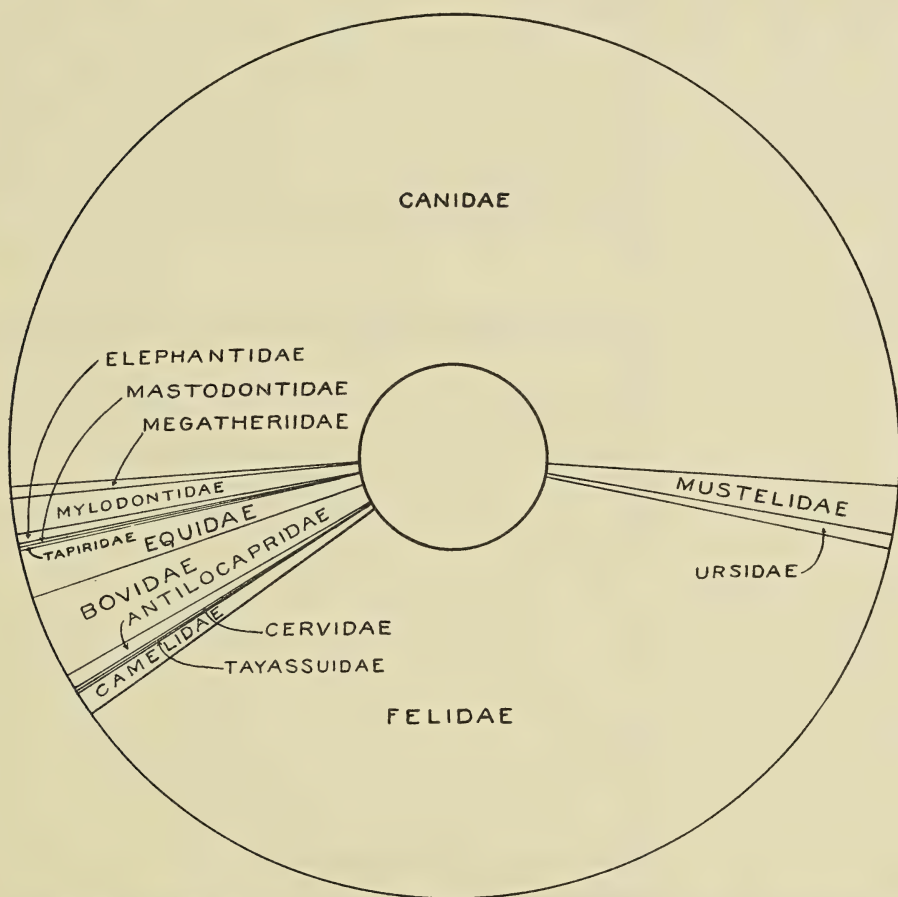


FIG. 5—Diagram showing relative number of individuals in the mammalian families (except rodents, lagomorphs, insectivores, and bats) occurring in the Rancho La Brea Pleistocene fauna.

yet been reported upon in a formal statement, and it is hoped that A. H. Miller's paper on this division of the McKittrick avifauna will precede in print the present report. Most of the accounts of the McKittrick birds list the total number of remains of each species as a basis for estimating relative abundance; while Howard (1930, p. 81)



* Includes *Parelephas* and *Archidiskodon*.

FIG. 6—Diagram showing number of individuals recorded for genera and species of mammals in the Pleistocene faunas of McKittrick (white bar) and Rancho La Brea (black bar). Rancho La Brea census after Stock (1929A).

has estimated the constituency of the Rancho La Brea avifauna by a method essentially comparable to that employed by Stock in his census of the mammalian assemblage. Furthermore, studies of the Rancho La Brea and McKittrick avifaunas are still being carried on so actively that it is futile to attempt at this time more than a general statement as to the constituencies of the two assemblages.

As has been noted already, the McKittrick avifauna is not an ecologic unit. Fauna number 1, which consists of nearly 1000 specimens, comprises 33 per cent anserines; 20 per cent limicolines; 14 per cent herons, storks, and cranes; the golden eagle 28 per cent; and all other land birds 5 per cent. As Miller (1925, p. 310) has noted, this assemblage suggests a widespread marshy area similar to conditions inferred at Fossil Lake. It should be noted that McKittrick avifauna number 1 comprises relatively more water birds than does Rancho La Brea (Miller, 1925, p. 310).

McKittrick avifauna number 2, on the other hand, is predominantly a land assemblage, and is quite similar to that of Rancho La Brea. Both the Rancho La Brea assemblage and the second McKittrick avifauna are characterized by relatively large representation of vultures and other raptorial types. In this connection it is interesting to note that the bird assemblage from the Southern California Academy of Sciences pit at Rancho La Brea (Howard, 1936, pp. 32-34) resembles McKittrick avifauna number 1, in that this excavation contains a relatively large percentage of water-dwelling types.

Combination of McKittrick avifaunas 1 and 2 shows that far less difference exists between the McKittrick and Rancho La Brea assemblages than when either McKittrick assemblage is considered alone. It is true, however, that aquatic types are slightly more abundant, relatively, at McKittrick, but this does not seem to have any age significance. Galliformes and owls are somewhat less abundant at McKittrick, but this discrepancy is probably due to a lighter forest cover in the vicinity of the McKittrick tar seeps. Since McKittrick avifauna localities 1 and 2 are separated by only one hundred feet, Miller's explanation that accumulation occurred near the shore of a lake and that avifauna number 2 is predominantly a land assemblage, seems entirely satisfactory.

Perhaps the most important difference in the avifaunas of McKittrick and Rancho La Brea lies in the relative abundance of the black vulture (*Coragyps*) and the American turkey vulture (*Cathartes*). At McKittrick *Cathartes* outnumbers *Coragyps* in a ratio of slightly more than five to one (Miller, 1935, p. 76); while at Rancho La Brea the extinct black vulture outnumbers *Cathartes* in a ratio of twenty to one (Howard, 1930, p. 84). As will be mentioned on a

following page, the relative proportions in representation of these raptors may have considerable age significance.

FACTORS GOVERNING GROUP REPRESENTATION

The factors governing the representation of animals in brea deposits are classifiable into three major categories, the first of which is capable of subdivision. They are: (1) environment, (2) time, and (3) chance and probability.

Since it is difficult, when dealing with asphalt assemblages, to separate environment and ecology, and still more difficult to distinguish between regional environment and the conditions which prevailed in the immediate vicinity of the pits, these factors are discussed to best advantage with climatic evidence in following sections.

The factor of time is so intimately associated with the problem of correlation, which in turn is related to environment and ecology, that a separate section has been set aside for its discussion. For the present it is sufficient to note that time seems to be of relatively little importance insofar as group representation is concerned. With regard to relative abundance of various groups, however, time seems to be the deciding factor, and on this basis it would appear that since modernized forms show greater abundance relative to extinct types at McKittrick, this occurrence is somewhat younger than Rancho La Brea.

With regard to the third factor, it is scarcely necessary to point out that since the Rancho La Brea mammalian assemblage in the collections of the Los Angeles Museum contains approximately twelve times as many individuals as that of McKittrick, absence of a specific type from the Los Angeles locality probably means that it did not inhabit the area during the period of fossil accumulation. However, in case of absence of a form from McKittrick, known to occur at Rancho La Brea, it is far less certain that it was absent from the area at a time when the tar seeps were active.

In view of rather scanty representation of the Felidæ at McKittrick, it is not surprising that certain forms such as *Smilodon californicus brevipes*, *Felis bituminosa*, and *Felis concolor* seem to be absent from the fauna, for these types are rare even at Rancho La Brea. Since the latter form still lives in the McKittrick area, it seems almost certain that chance alone is responsible for its absence in the fossil assemblage.

The McKittrick Canidæ, on the other hand, are a relatively abundant group. Why certain of the Rancho La Brea forms, *Canis andersoni* and *Canis occidentalis furlongi*, should be absent from the former locality is difficult to explain. Both forms are rare at Rancho La Brea and never seem to have been present in the California area in great numbers. Consequently, their absence in the McKittrick

tar beds may be due to chance. On the other hand, isolated and fragmentary specimens of both forms mentioned above are not readily determinable, but it is certain that no skull material is available. Since foxes are not abundant at either Rancho La Brea or McKittrick, absence of *Urocyon* at the latter locality may well be due to chance. As Stock (1929A, p. 289) has indicated, it may be that absence of *Vulpes* at the Los Angeles locality is to be attributed to more humid conditions than those now prevailing in the area.

While the habits of *Nothrotherium* are not sufficiently well known to permit a reasonable inference as to the environmental conditions permitting its presence, the sparse representation of ground sloths at McKittrick indicates that absence of this form from the San Joaquin Valley locality is likewise the result of chance.

The Elephantidæ are not well represented at McKittrick, and absence of *Archidiskodon imperator* from the collections seems reasonably to be attributed to the same factor presumed to be responsible for the non-occurrence of *Nothrotherium*.

In view of their scarcity at Rancho La Brea, absence of representatives of the Tapiridæ at McKittrick seems due to accident.

While it is probably true that a large proportion of the McKittrick rodents are Recent in age, time alone does not seem to offer sufficient reason for their relative scarcity at Rancho La Brea. Sufficient attention may not have been directed to these forms to obtain adequate collections from the latter locality. In view of the large number of very small bones of passerine birds obtained at this locality, however, this explanation is not very satisfactory. Some unknown factor in local environment may account for the rarity of rodents at Rancho La Brea.

As at Rancho La Brea, a conspicuous absence of all members of the Procyonidæ is noted in the McKittrick fauna. As Stock (1929A, pp. 288-289) has suggested, the extreme wariness of these animals may be responsible for their absence in the tar deposits.

Factors governing representation of the birds have already been touched upon on page 142. There remain, however, some outstanding exceptions which deserve mention.

Miller (1935, pp. 74-75) noted the absence of *Parapavo* at McKittrick, and concluded that there was too little cover in the area for so large and conspicuous a galliform as the wild turkey. The same author (1935, p. 75) suggested that the factor of latitude may account for the apparent limitation of *Morphnus woodwardi* to the deposits of Rancho La Brea. The same factor was suggested by Miller (1935, p. 76) as an explanation for the apparent rarity of *Coragyps* at McKittrick. However, as this author pointed out, its near relative, *Coragyps shastensis*, is found in the Pleistocene caves several hun-

dred miles to the north. No explanation was offered by Miller for rarity of *Cathartes aura* at Rancho La Brea.

Howard and A. H. Miller (1933, p. 17) demonstrated that at Conkling Cave, New Mexico, *Coragyps* predominates over *Cathartes*, while at Shelter Cave in the same state *Coragyps* is absent and *Cathartes* is abundant. These authors suggested that since in most Pleistocene deposits *Coragyps* predominates over *Cathartes*, Shelter Cave may be younger than Conkling Cave. Wetmore (1931, p. 25) also noted the abundance of *Coragyps* in the Pleistocene of Florida. As is stated on page 149, at McKittrick *Cathartes* is much more abundant than *Coragyps*; while at Rancho La Brea (Howard, 1930, p. 84) the reverse is true. Following Howard and Miller's suggestion, it would appear that on this basis McKittrick is younger than Rancho La Brea.

Miller (1935, p. 76) held the entire absence of the California condor, *Gymnogyps californicus*, from the McKittrick tar seeps to be inexplicable. This species is found in great numbers at Rancho La Brea, and still lives within sight of the McKittrick locality.

With regard to other raptors, Miller (1935, p. 77) pointed out that in McKittrick avifauna number 2 among three genera *Aquila* comprised 65 per cent, *Urubitinga* 29 per cent, and *Neogyps* 5 per cent. At Carpinteria *Neogyps* outnumbered *Aquila* by two to one, while *Urubitinga* was more abundant in one exposure and less in the other. Miller stated that McKittrick thus comes to resemble Rancho La Brea, and is in sharp contrast to Carpinteria. The explanation offered by this author is that at the time of fossil accumulation Carpinteria was a wooded area.

A. H. Miller has informed the writer that the northwest crow, *Corvus caurinus*, is definitely absent at McKittrick. In Miller's opinion this form was then as now a coast-living bird. Consequently, absence of this form has no climatic significance.

ECOLOGICAL AND ENVIRONMENTAL FACTORS AT McKITTRICK AND RANCHO LA BREA

In preceding sections all seemingly pertinent data relating to the McKittrick fossil assemblage have been presented with a minimum of interpretation. It is now necessary to re-examine the evidence with a view to sorting out the following factors: regional environment and ecology as contrasted with local ecology and environment; climate as distinguished from environment; and chronology. Since the second proves to be the most highly inferential, it has been left to the last. In this section only the first factor will be considered.

The combined evidence of the mammals, birds, and plants indicates that during the period of fossil accumulation the regional environment at Rancho La Brea and McKittrick was much the same as that of today. In both instances the physical environment consisted of

broad and perhaps rather arid plains, which bordered directly upon rugged mountain ranges. Since the McKittrick fossil deposit is located nearer to the uplands, it is possible that absence of certain mammals at Rancho La Brea is to be attributed to greater distance of this locality from the Santa Monica Range. *Tanupolama* and *Preptoceras*? are cases in point. In any event, it seems reasonably certain that neither of these forms ranged into the Los Angeles area during the period of fossil accumulation. Contrasted with these dissimilarities are those which may be due to fundamental differences in mode of accumulation at McKittrick and Rancho La Brea. The factors involved in the latter may be designated as local environment as distinguished from regional environmental conditions.

Nothing is more apparent than that the Rancho La Brea assemblage is an abnormal and ecologically impossible one. This is shown by the extraordinarily high percentage of carnivores: over 90 per cent in the case of the mammals, and approximately 67 per cent in the case of the birds. It is almost equally apparent that the McKittrick assemblage is a more normal one from an ecological standpoint, for only 59 per cent of the mammals and a slightly higher percentage of the birds are carnivorous. Reasons for this discrepancy are to be sought perhaps in differences in the two types of traps involved. The seeps at Rancho La Brea seem to have been very efficient traps, in which a considerable number of animals were more or less continuously snared. The surface flows at McKittrick may have congealed periodically, and thus were not so often an active death-dealing agent in entrapping creatures. In addition, presence of large bodies of water may have served to conceal victims of the tar from flesh-eaters. Under these conditions it is conceivable that carnivorous types were not attracted to the McKittrick seeps in numbers comparable to those that must have haunted the borders of the Rancho La Brea tar pools. Although some time difference may exist between the two asphalt assemblages, it would appear that this factor plays only a subordinate part insofar as relative abundance of carnivorous and non-carnivorous types in areas not immediately adjacent to the tar seeps is concerned. There likewise appears to be no ecologic reason why raptorial forms should have been over-abundant in the region of Rancho La Brea, and it seems necessary to conclude that environmental conditions in the vicinity of the tar seeps are responsible for the poorer representation of flesh-eaters at McKittrick. Since the relative abundance of carnivores at the latter locality is considerably higher than normal, it would appear that trapped herbivores offered some bait for such types.

Two closely related problems are the relative abundance of saber-tooth and true cats, and the numerical representation of dire wolves in proportion to other members of the dog family. At Rancho La Brea

Ænocyon far outnumbers all other canids; while *Smilodon* outnumbers *Felis atrox* in a ratio of approximately thirty to one. It should be noted, however, that in some of the pits—numbers 67, 61, 60, 13, and 4 of the Los Angeles occurrence—*Felis atrox* actually outnumbers *Smilodon*. This may be due to nothing more than chance, but it may indicate an age difference between these and other pits. As Merriam (1912, pp. 255-256) has shown, the dire wolves appear to have been persistent predators of the tar seeps; while the coyotes, which depend upon smaller animals and birds for their prey, do not appear to have frequented the traps to so great an extent as their larger relatives. A similar relation seems to have existed in case of the saber-tooth and true cats. As has been indicated by Merriam and Stock (1932, p. 21), *Felis atrox* apparently did not visit the tar pools so often as did *Smilodon*. The conclusion seems justified that even at Rancho La Brea, *Felis atrox* and the smaller dogs may have actually outnumbered *Smilodon* and *Ænocyon* in areas away from the tar pits. If this is true, the greater normality of the McKittrick assemblage is again emphasized.

Since fewer large herbivores, such as ground sloths and mastodons, occur at McKittrick than at Rancho La Brea, it is possible that large carnivores like *Smilodon* were not attracted to the former area. However, this assumption does not explain the dominance of *Felis atrox*.

It is also possible to interpret these data as indicating a time difference between the two faunas. If it is assumed that McKittrick is older than Rancho La Brea, it is conceivable that *Smilodon* and *Ænocyon* had not yet been forced by racial senility to seek an easier prey as represented by trapped animals in tar pools. An alternative view is that McKittrick is younger than the Los Angeles occurrence, and that only the last survivors of these gradually disappearing races are found there. Of the three possibilities, the latter seems preferable, but none appears as probable as the alternative first offered.

With regard to birds, as has been mentioned on page 142, nearly all major discrepancies between the avifaunas of McKittrick, Rancho La Brea, and Carpinteria may be accounted for on the assumption that Carpinteria was a well wooded area, Rancho La Brea less so, and that McKittrick was practically devoid of trees. The somewhat better representation of water birds at McKittrick leads to the conclusion that during the period of fossil accumulation, the tar seeps were near the margin of a lake or marshy area. Singularly enough, this feature of the local environment seems to have left no recognizable impression upon the mammalian fauna.

Very little can be said with conviction concerning the ecology, except that when suitable allowance is made for peculiar environmental conditions in the immediate vicinity of the tar pits, nearly all factors

with the following important exception seem to have been much like those of the present. With decline and disappearance of the large herbivores the large carnivores might well be expected to die out, and this seems to be true in the case of the McKittrick fauna. Since this process was presumably a gradual one, a purely ecologic factor takes on considerable chronological significance.

A few mammalian species, *Thomomys bottæ bottæ* and *Mustela frenata nigriauris*, found at McKittrick are slightly out of their present range, but this does not necessarily indicate an important change in environment or climate.

AGE AND CORRELATION OF THE MCKITTRICK FAUNA

In the preceding section it has been pointed out that insofar as mammalian and avian faunas are concerned, there seems to be scant reason for considering McKittrick and Rancho La Brea as other than closely related in time. Outstanding discrepancies can be attributed to either environmental or ecological factors. However, the method used so far cannot be expected to give precise results. It remains to examine the faunas more in detail in order to determine, if possible, the age relations of the asphalt faunas and the part of Pleistocene time to which they belong.

Stock (1929A, pp. 286-287) has suggested that should another large brea fauna be found, its time relations with Rancho La Brea might be determined by a comparison of relative abundance of extinct and living forms. This method assumes that extinction was a gradual rather than a sudden process and, furthermore, that environmental conditions around individual tar beds were identical. The first assumption seems very probable, but the second involves difficulties when applied to McKittrick and Rancho La Brea. As indicated on page 153, it seems probable that conditions of entombment at McKittrick were such as to bring about a relatively poor representation of extinct carnivores. Since members of this order furnish the most convenient basis for comparison, it is impossible to conclude from this evidence alone whether relatively greater abundance of modernized carnivores at McKittrick indicates that this deposit is actually younger than Rancho La Brea, or that in areas away from the tar seeps *Smilodon* and *Ænocyon* were not nearly so abundant as a census of the Rancho La Brea fauna seemingly indicates. As shown by figure 6, however, the relatively small number of McKittrick carnivores includes almost as many modernized forms as does the entire Los Angeles Museum collection from Rancho La Brea. Unless an unduly large proportion of the McKittrick canids are post-Pleistocene in age, it would appear that an age difference exists between the two localities and that McKittrick is a somewhat younger stage.

Here it should be recalled how several sources of evidence suggest that the above conclusion is correct. At McKittrick *Cathartes* is relatively more abundant than *Coragyps* and among mammals *Antilocapra* is better represented than *Capromeryx*. At Rancho La Brea the reverse is true. Furthermore, both in percentage of extinct species and in the relative abundance of these forms Rancho La Brea exceeds McKittrick. Therefore, it seems necessary to conclude that McKittrick is somewhat younger than Rancho La Brea, but in view of the relatively slight differences as measured by ordinary standards, the age difference does not appear to be greater than a single glacial or interglacial epoch. In this connection it seems desirable to determine, if possible, to what epoch of the Pleistocene Rancho La Brea belongs.

Since it cannot be definitely determined whether or not the fauna of Rancho La Brea is ancestral to that of McKittrick, a contingency more often considered by invertebrate than vertebrate palæontologists deserves mention, namely, might not the two occurrences be contemporaneous and the predominance of modernized forms in the McKittrick assemblage be due to invasion from some other area? It is difficult to see how this hypothesis might account for the representation of *Coragyps* and *Cathartes*; and furthermore, there is no known ecologic reason why such modernized forms as *Antilocapra* should be more abundant in one area than in another. In order to bring about the relative order of abundance in the two faunas through invasion it is necessary to postulate that migration of modernized forms into the McKittrick area was for some unknown reason easier than into the Los Angeles region. While this may be true, the burden of proof seems to rest with the advocate of this hypothesis.

In his comprehensive review of the geology of the Rancho La Brea occurrence Merriam (1911, pp. 206-208) pointed out that the alluvial deposits which contain the Rancho La Brea fauna may interfinger with marine beds of Upper San Pedro age, and I have been informed by petroleum geologists that later drilling has actually proved this to be the case. It was stated, furthermore, that the fossil-bearing continental deposits had their origin from detritus carried down by streams since the last uplift of the Santa Monica Mountains. The only subsequent event has been formation of a series of stream terraces, which has caused some erosion of the fossil-bearing alluvium. Although the epoch of Pleistocene time represented by the Rancho La Brea fossil assemblage was not stated specifically, by implication it appeared to be the early part of that period, for the Upper San Pedro beds were then regarded as belonging to the Aftonian, or first interglacial epoch.

For various reasons Hay (1927, pp. 189, 199, 216) considered both Rancho La Brea and McKittrick to belong to the Aftonian. The relation of the alluvial deposits of Rancho La Brea to the Upper San Pedro marine beds was stressed by this writer to a far greater extent than by Merriam, but no incontrovertible proof of Aftonian age was offered. However, at that time it was still the opinion of many workers that the Upper San Pedro beds belonged to the first interglacial epoch.

In a discussion of the geology of the Santa Monica Mountains Hoots (1930, pp. 126-130) considered that the last uplift of the range occurred in late Pleistocene time. The evidence cited for this conclusion is mainly physiographic. The trend toward a later date for uplift of the California Coast Ranges is noteworthy and has continued to gain support.

During recent years, a strong tendency to refer the Upper San Pedro or Palos Verdes beds, as they are now called, to the late Pleistocene has developed. It is unfortunate that evidence for these conclusions has not yet been fully published, but Woodring (1933, p. 36) has suggested that the Palos Verdes beds should be referred to the Sangamon, or last interglacial epoch. Since this conclusion seems likely to be substantiated, it is important to inquire if there is any aspect of the vertebrate faunas of Rancho La Brea and McKittrick which cannot be harmonized with so relatively late an age.

The writer (1937, pp. 95-96) has stated his objections to Hay's correlations in a previous article, and it is only necessary to point out that all of the forms which Hay considered to be characteristically Aftonian have been found in beds of late Pleistocene age (Romer, p. 75). Consequently, insofar as ranges of vertebrates are concerned, there seems to be no reason why the Rancho La Brea Pleistocene assemblage should be regarded as any older than the Sangamon, or last interglacial epoch. Since there is some evidence that McKittrick is younger than the Los Angeles occurrence, it would follow that this assemblage is Wisconsin in age. The fauna of Carpinteria seems more closely related to McKittrick than to Rancho La Brea, and may range into the sub-Recent.

Consequences of the above correlations and age determinations are worthy of note. Perhaps most striking of all is the conclusion that if these so-called early Pleistocene assemblages are actually late Pleistocene in age, early Quaternary vertebrate faunas are as yet practically unknown in western United States. This problem was discussed in some detail in an earlier paper by the writer (1937, pp. 86-98), and it was suggested that some of the so-called late Pliocene faunas may be referred more properly to the early part of the Pleistocene.

A small collection of fossil vertebrates from Astor Pass, near Pyramid Lake, Nevada, was described by Merriam (1915) and compared with the Rancho La Brea fauna. Since, as Merriam indicated, this assemblage is very similar to that of the Los Angeles occurrence, and since the Astor Pass fauna can be correlated with one of the stages of Lake Lahontan, it is now possible to reconcile the vertebrate evidence with the opinion of Antevs (1925, pp. 76-77) and perhaps even with that of Jones (1925, p. 47) as to the relatively late age of the lake.

The relatively late date for uplift of the California Coast Ranges necessitated by this view is in accord with nearly all recent work excepting that of Davis (1933). This investigator has sought to correlate marine terraces on the southern flanks of the Santa Monica Mountains in the vicinity of Santa Monica Bay with changes of sea-level incident to glacial and interglacial climatic changes. Such an interpretation would necessarily place uplift of the range in early or middle Pleistocene time. However, in a tectonically active region such as southern California it would be surprising if this interpretation should eventually prove correct, for in the Palos Verdes Hills a short distance to the south, marine terraces occur which cannot be correlated with those of Santa Monica Bay. Consequently, it would appear reasonable to ascribe the terraces in the latter region to diastrophism, for in the Palos Verdes Hills there are too many terraces to be accounted for by changes of sea-level. That the Santa Monica terraces may be of rather late Pleistocene age is suggested by Woodring's work (1935) in the Palos Verdes Hills. This author finds that fossils from terraces west of the city of San Pedro are essentially the same forms as those inhabiting the Pacific Ocean today. A late-middle to early-late Pleistocene age is suggested for the lowest terrace.

Finally it can be said that if the above views are substantiated by future studies, a somewhat new conception of sequence of Pleistocene vertebrate faunas seems necessary. In this connection, the work of Hall (pp. 44-46) is a valuable contribution.

CLIMATIC CONDITIONS DURING THE PLEISTOCENE ACCUMULATION AT MCKITTRICK AND RANCHO LA BREA

The ideal correlation of the asphalt faunas is to establish their position in the glacial-interglacial sequence established in the glaciated areas. This can scarcely be done without some knowledge of climate of the times, and any attempt to arrive at a defensible interpretation of the Pleistocene climate of an area situated in the latitude of California encounters many difficulties. A desire to point out some of these complications rather than a hope to reach a final conclusion has led to a formulation of the following statement.

Perhaps the most serious obstacle is that climatologists are not yet agreed as to the influence exerted on climates of unglaciated areas by glacial and interglacial conditions in northern latitudes. Brooks (1925, p. 30) supports the view that glacial epochs in northern latitudes are accompanied by pluvial periods in tropical and sub-tropical areas. Milankovitch (1930, p. A137), on the other hand, contends that during epochs of glaciation arid to semi-arid conditions prevailed. The present discussion does not aim to reconcile these conflicting views or to indicate a preference. It is merely intended to demonstrate that many of the apparent discrepancies in the climatic evidence furnished by the asphalt faunas are not necessarily inconsistent with the correlations proposed in this paper.

McKittrick is at present in the rain-shadow belt which extends along the lee side of the Coast Ranges, and this must have been true ever since the mountains reached a sufficient elevation to disturb passage of moisture-laden winds coming from the Pacific Ocean. Rancho La Brea, on the other hand, is situated on the seaward slope of the Coast Ranges, and it is possible that changed meteorological conditions of the Pleistocene may have influenced the climate of the area. Just what this effect on the Rancho La Brea area was, is at present difficult to evaluate, but it seems reasonable to suppose that even during a glacial epoch, the climate of McKittrick was relatively dry.

Turning now to the fossil evidence, the climate of Rancho La Brea has been a subject of some disagreement among palæontologists. L. H. Miller (1912, pp. 103-105) suggested that the climate during Rancho La Brea time was somewhat warmer and more humid than at present. The inconclusive nature of the evidence was fully recognized by this author. Frost (1927, pp. 85-87) concluded from evidence of the plants that the climate was somewhat cooler and with a rainfall of approximately fifteen inches. Merriam and Stock (1932, p. 26) likened conditions to those prevailing on the South African veldt at the present time, although a slightly more humid climate was considered probable. Compton (1937, pp. 88-89) from a study of the shrews from the asphalt concluded that the climate of Rancho La Brea was warmer and drier than at present and supported this view with a note by Mason concerning the plants. The latter author states that preponderance of *Juniperus* of a species now found in the Tehachapi Mountains and absent on the coast should be conclusive. From the above there appears to be a tendency to regard the Rancho La Brea assemblage as existing under an arid to semi-arid climate characterized by relatively high temperature. This view agrees with the evidence of a warm water environment furnished by the Upper San Pedro marine assemblage. Whether this conclusion can be cited

as evidence that the Rancho La Brea fauna lived during an interglacial stage remains an open question, but there seems to be some evidence opposed to this view.

A. H. Miller (1929, p. 19) has pointed out that presence of the northwest crow, *Corvus caurinus*, at Rancho La Brea seemingly indicates cold conditions. This interpretation may eventually be modified. Presuming it to be correct, it is still possible to reconcile this evidence with the general climatic picture, if it is granted that the Rancho La Brea deposition extended into an epoch of glaciation. From the character of the seeps this contingency is not only possible but even probable. The timber wolf, *Canis occidentalis furlongi*, may also indicate a rather cold climate, but in this instance it is probable that the wolf is more closely related to forms still inhabiting western United States than to those of the plains of Canada.

As stated on a preceding page, the evidence for considering the climate of Carpinteria as relatively humid, and perhaps somewhat cooler than at present, is particularly well established. It also seems plausible to correlate the southward extension of the Monterey Pine Forest with an epoch of glaciation. Since Carpinteria is apparently of same age as McKittrick, one may conclude that similar climatic conditions prevailed at the San Joaquin Valley locality. This, however, does not seem to be true.

As has been mentioned already, the McKittrick fossil rodent fauna suggests the presence of climatic conditions comparable to those of today. In oral communications A. H. Miller¹ has stated that this is suggested by the passerine birds and H. L. Mason that it is likewise indicated by the plants. Abundance of anserines at McKittrick is suggestive of humid conditions, but as discussed on page 131, it seems reasonable to assume that Lake McKittrick came into existence and disappeared through physiographic causes. Consequently, abundance of water-fowl at this locality may be somewhat misleading insofar as climatic inferences are concerned and one may reasonably conclude that the area was then as now in the rain-shadow belt. It is apparently not inconsistent to correlate the dry interior plant assemblage of McKittrick with the humid coast forest of Carpinteria. Furthermore, there is no important climatic reason why both should not be referred to the Wisconsin glacial epoch.

When it is recalled that a traverse of the Coast Ranges of Oregon from the Pacific Ocean to the central part of the state shows a similar contrast at the present time, the correlation made above does not seem improbable. It is perhaps worthy of note that today the cli-

¹ While this paper was in press Miller's article (1937) on the biotic conditions suggested by the avian assemblages of the tar pits appeared. The conclusions arrived at by Miller are essentially the same as those offered in these pages.

mate of Carpinteria is somewhat more humid than that of the McKittrick area.

Several facts tend to argue against the above interpretation of the climate of the McKittrick area. First of all, the northwest crow, which might reasonably be expected in the fauna, is, as I am told by A. H. Miller, definitely absent. However, this same authority believes that this crow was then as now a coast species which never ranged into the dry interior belt of McKittrick. Absence of the timber wolf is so inconclusive that this alone does not seem sufficient evidence to overthrow the major conclusion, for its absence is offset by presence of *Preptoceras*?. This form shows musk-ox affinities, and would thus tend to indicate relatively low temperatures. However, there is a strong probability that at McKittrick, as at Rancho La Brea, deposition extended into both a glacial and an interglacial stage.

SYSTEMATIC DESCRIPTION

Since most of the mammals found in the McKittrick asphalt are adequately described from other localities, only new or controversial species are treated in detail. In all cases, however, an attempt is made to indicate the principal reasons for specific reference of the form in question.

The McKittrick occurrence is entered in the field records of the Division of Palæontology, California Institute of Technology, as locality 138; while in the records of the Museum of Palæontology, University of California, this locality is given as number 7139. No further reference to locality numbers will be made.

For purposes of reference the California Institute of Technology is cited as C.I.T. and University of California is cited as U.C. Specimens listed by number alone, or preceded by the letters C.I.T., are from the collections of the California Institute. The letters M.V.Z. refer to the Museum of Vertebrate Zoology, University of California. All numbers preceded by the letters D.C. refer to specimens in the Dickey Collection of Recent Mammals, California Institute of Technology.

References to J. C. Merriam are usually cited by surname only; while those to C. Hart Merriam are always by surname accompanied by initials.

FELIDÆ

In contrast to Rancho La Brea, McKittrick has relatively few representatives of the cat family. Three of the Rancho La Brea forms—*Smilodon californicus brevipes*, *Felis bituminosa*, and *Felis concolor*—are not found at McKittrick, and the types that are present are far less abundant relatively than at the Los Angeles locality. Reasons for this difference are discussed on pages 153–154. It is also of interest to find, as is shown in figure 6, that at McKittrick *Felis atrox* apparently outnumbers *Smilodon*.

Smilodon californicus Bovard

The skull and mandible of a mature individual, No. 650 C.I.T., Plate 2, with teeth badly broken, associated skeletal parts, and a few additional cranial elements represent the saber-tooth cat. As noted by Merriam and

Stock (1932, p. 225), the skull almost equals in size that of the largest individuals from Rancho La Brea, and even exceeds the latter in certain dimensions. Among these measurements width of skull and thickness of ramus seem to be the most important. There appears to be little doubt, however, as to the specific identity of the McKittrick and Rancho La Brea smilodonts.

Felis atrox Leidy

The great lion-like cat is represented in the California Institute collections by two fairly complete skulls and mandibles, in addition to various skeletal elements (see Plate 3). Both skulls represent mature individuals, for the sutures are closed and the teeth rather worn. No. 648 lacks only the incisors and M₁, while No. 649 is practically complete. The former is remarkable for its large size, for it approaches the larger individuals from Rancho La Brea in nearly all measurements and equals the largest in width across the zygomatic arches. No. 649 is much smaller than No. 648, and is below the average of the Rancho La Brea forms in size. However, it compares closely in measurements with No. 2900-18 from that locality. It seems probable that the size difference between the two McKittrick individuals represents a variation due to sex.

Other skeletal elements comprise numerous vertebrae, a right humerus, three tibiae, two radii, a fibula, an ulna, a large right femur, as well as various carpal and tarsal elements.

Felis daggetti Merriam

An incomplete and somewhat distorted skull, No. 29524 U.C., Plate 4, figs. 1, 1a, is the only representation of this species. As indicated by Merriam and Stock (1932, pp. 225-226), the dentition is exceptionally heavy, nearly all tooth dimensions being in excess of those of the type of *Felis bituminosa*. In P₃ the postero-external corner of the crown is prominently developed. Merriam and Stock conclude that No. 29524 may represent a large male individual of the *Felis bituminosa* group or it may be more nearly related to *Felis daggetti*. The specimen was provisionally referred to the latter species.

Lynx rufa cf. *fischeri* Merriam

Part of a right mandibular ramus, No. 2040 C.I.T., Plate 4, figs. 2, 2a, which lacks the anterior lower premolar is referred to this subspecies. Since the condyle in this specimen is also lacking, the most important characters which distinguish *Lynx rufa fischeri* from *Lynx canadensis* are not available. The specimen is referred to the former variety largely because of close agreement between the two in nearly all measurements. In this connection see table 5 below.

A left mandibular ramus in the collections of the University of California approximates the type of *L. r. fischeri* even more closely in nearly all measurements than the California Institute material.

U.C. No. 33113 consisting of an immature mandible with milk-teeth corresponds very closely to two immature specimens of the Recent *Lynx rufa californicus* in the collections of the Museum of Vertebrate Zoology, University of California. It is possible that the McKittrick lynx represents the living rather than the extinct variety, but it seems improbable that any difference exists in milk-dentitions of *Lynx rufa fischeri* and *Lynx rufa californicus*.

TABLE 5—Measurements (in millimeters) of *Lynx rufa* cf. *fischeri*

Mandible	McKittrick 2040	Type * U.C. 11287
Length from posterior side of canine alveolus to posterior side of M1.....	36	33.9
P4, anteroposterior diameter.....	8.9
M1, anteroposterior diameter.....	11.5	11.2
Height of mandible below protoconid of M1.....	15.9	12.2
Thickness of mandible below protoconid of M1.....	6.8	7.5

* Rancho La Brea collection measurements after Merriam and Stock (1932).

CANIDÆ

Since Merriam's early work on the Canidæ of Rancho La Brea considerable information regarding modern forms of the California area has accumulated. In addition, the dogs of Rancho La Brea have been the occasion of comment by various authors, and already a confusing amount of synonymy has resulted. In order to clarify the issue, it is necessary to review the status of the Rancho La Brea forms.

Notes on the Status of the Genus Ænocyon.—This genus was founded by Merriam, who listed the following characters:

"The generic characters of *Ænocyon* are found in the massiveness of skull and dentition, extreme overhang of the inion, shortness of the basicranial region posterior to the glenoid fossæ, massiveness of the upper and lower carnassials, reduction of the hypocone of M1, and probably in characters of the skeleton not as yet available from other material than that obtained at Rancho La Brea."

To this genus Merriam referred the following species: *Ænocyon dirus* (Leidy), *A. ayersi* (Sellards), and *A. milleri* (Merriam).

Although his objections to *Ænocyon* as a genus do not appear to have ever been stated definitely, W. D. Matthew continued to refer these forms to *Canis*. The McKittrick material offers little evidence of value as to the status of the genus. However, the occurrence of both *Ænocyon dirus* and *Ænocyon milleri* at the San Joaquin Valley locality tends rather to confirm the existence of two distinct species of dire wolves in the Pleistocene of western North America. Since one of the principal reasons for Merriam's reluctance to establish a new genus for *A. dirus* was the apparent lack of specific differentiation in the group, this objection does not appear valid. From the writer's point of view, although *Ænocyon* may not be of rank equivalent to that of other canid genera and may eventually be reduced to a subgenus, it furnishes a convenient grouping for the large Pleistocene wolves.

Notes on the Status of Canis occidentalis furlongi.—Merriam (1912, p. 251) separated this form from the living *Canis occidentalis* on the basis of relatively narrower muzzle, heavier superior carnassial, and relatively narrower anteroposterior diameter of M2 seen in the Rancho La Brea form.

Hay (1927, p. 184) expressed a desire to elevate this form to specific rank. To quote from Hay:

"The dog designated as *Canis occidentalis furlongi* by Dr. John C. Merriam appears to the present writer as better given specific rank. The name *C. occidentalis* has been restricted by Gerrit S. Miller (Smiths. Misc.

Coll., vol. 59, 1912, No. 15, p. 4) to the wolf inhabiting the plains of Canada from Saskatchewan to the Arctic coast. It is improbable that it or a subspecies of it was present at La Brea during the warm early Pleistocene. I find no other large *Canis* which has, so far as we know, inhabited that region. I see no good reason why *C. furlongi* should not for the present be regarded as a distinct species."

Although the McKittrick fauna does not contribute directly to this question, in light of present knowledge Hay's arguments do not appear very convincing. In view of the amount of individual variation known to occur in recent species, it seems best to retain Merriam's status. A question here involved relates particularly to the distinctiveness of *Canis occidentalis furlongi* from the living form. For the present it seems desirable to regard the Rancho La Brea wolf as a distinct subspecies.

Notes on the Status of Canis ochropus orcutti.—This coyote from Rancho La Brea was originally described as *Canis orcutti* (Merriam, 1910, p. 391). At a later date Merriam (1912, pp. 255-258) changed the designation to *Canis ochropus orcutti*. The subspecific characters were listed as follows:

"The skulls of *C. o. orcutti* average somewhat larger than in the living *C. ochropus*, and are noticeably broader across the palate and zygomatic arches. The mandible is considerably higher, particularly below the molars, and is also thicker transversely than in the living form in this region . . ."

In 1927 Hay (p. 184) listed this form under the original title of *Canis orcutti*. No comment was given. In view of the above statements concerning the status of *Canis occidentalis furlongi* it would appear that revision of the fossil coyote is likewise unwarranted.

Grinnell (1933, pp. 112-114) recognizes four races of the genus *Canis* in the California area. *Canis ochropus* Eschscholtz is now a synonym of *Canis latrans ochropus*, the coyote inhabiting most of the state west of the Sierra Nevada. Intergradation with other races is very common, as is variation of subspecific characters. Grinnell states that variation is especially marked in characters of skull and teeth.

Until the extent of individual and secondary sex variation among Recent coyotes is determined by mammalogists it appears futile to attempt to establish the status of *Canis ochropus orcutti* (= *C. latrans orcutti*). After a somewhat cursory examination of approximately two hundred skulls of *Canis latrans ochropus* in the Museum of Vertebrate Zoology, University of California, the writer was unable to recognize definitely any constant secondary sex variation in either skull or tooth characters. Variation in size and pattern of the teeth, however, is extremely common, and of so marked a nature that on these characters alone a palæontologist might establish several distinct species. There appears to be little doubt, however, that the Rancho La Brea coyotes are correctly referred to the species *C. latrans*, although subspecific reference is still a matter of doubt. With exception of very old male individuals, few modern specimens of *Canis latrans ochropus* equal the Rancho La Brea form in width of muzzle and massiveness of the lower jaw. In addition, the dentition of the latter is also somewhat heavier than that of the modern form. Consequently, pending a fuller report on the coyotes, it seems advisable to retain *Canis latrans orcutti* as a distinct subspecies.

In both the McKittrick and Rancho La Brea collections are coyotes that cannot be distinguished from Recent *C. latrans ochropus* on the basis of available material and this fact was fully appreciated by Merriam (1912, p. 258) in his study of the Rancho La Brea specimens. Merriam therefore

concluded that the designation *Canis latrans orcutti* suited the entire series better than recognition of the presence of two subspecies at Rancho La Brea. Although the period of fossil accumulation at McKittrick and Rancho La Brea may have been long enough to permit evolution of one subspecies into another, this interpretation does not seem so plausible as does the inference that during late Pleistocene time the range of individual variation within a subspecies was somewhat greater than now. Since there are at present no data of value for choosing between these alternatives, less confusion might arise in the minds of future workers were the second hypothesis accepted and were all of the McKittrick coyote material referred to the subspecies *Canis latrans orcutti*. In order to place the evidence before the reader, the McKittrick coyotes are described in some detail in the hope that future studies may lead to a satisfactory clarification of this group.

Canis latrans orcutti Merriam

Of the twenty-three nearly complete skulls in the collections of the California Institute of Technology, five, Nos. 2041-2045, Plate 5, are characterized by somewhat more massive dentition, larger size, and broader muzzle than is the case for average skulls of the existing *Canis latrans ochropus*. The remaining eighteen, Nos. 2046-2063, Plate 6, fall within range of variation of the living species.

Three mandibular rami, Nos. 2064-2066, are characterized by massive dentition, noticeable thickness below M₁, and prominent convexity in the region of the first lower molar. These features agree closely with those of the Rancho La Brea form. On the other hand, eight mandibular rami, Nos. 2067-2074, show no characters wherein they can be distinguished from the living form.

Except for character of size, the lower teeth seem to show relatively little individual or subspecific variation. The upper teeth, however, exhibit such a striking variation of characters that were it not true that a similar range can be seen in a large series of the modern species, several distinct species or subspecies might be established on the basis of the McKittrick material.

One mature skull, No. 2046, Plate 7, in the McKittrick collection is characterized by a massive dentition and a peculiar M₁. In this specimen the first molar shows an extraordinarily large hypocone which continues without interruption around the antero-internal margin of the tooth where it is connected with the cingulum. Thus, a tooth pattern is developed which is more characteristic of *Canis occidentalis furlongi* than of *Canis latrans*. This specimen was at first thought to represent a distinct species until it was discovered that it corresponds in all respects, except that of size, to a mature male specimen of *C. l. ochropus*, M.V.Z. No. 12687, from West Riverside, California.

Individuals from Rancho La Brea comparable to the above are L.A. Mus. specimens Nos. 3200-46 and 3200-5.

In all remaining specimens there is, as is shown by tables 6 and 7, considerable variation in size. The most striking variation, however, is seen in the pattern of M₁. This is most marked in shape of the internal lobe and in size and shape of the hypocone. It is worthy of note that in both the *orcutti* and *ochropus*-like individuals approximately the same degree of divergence from the normal is exhibited. In a majority of cases the internal lobe is relatively narrow anteroposteriorly, while the hypocone is quite small, and does not extend forward to the anterior margin of the tooth.

Although size and shape of the remaining tooth cusps also show minor variations, divergences of these cusps from the normal are insignificant compared with variation seen in the hypocone. It is true that there are in

TABLE 6—Measurements (in millimeters) of skull, mandible, and dentition of *Canis latrans orcutti*

Skull	McKittrick			Rancho La Brea
	2041	2042	2043	U.C. No. 10842 (small sp.)
Length from anterior end of premaxillary to posterior end of condyles.....	194 ^{ap}	186 ^{ap}	198	188.5
Length from posterior side of \bar{C} to posterior side of M_2	78	78.5	82.6	80.5
Length from anterior side of P_4 to posterior side of M_2	40 ^{ap}	41	40.8	37.3
Least width of muzzle between \bar{C} and P_4	36.8	35	36.8	
Width across zygomatic arches.....	112 ^{ap}	108
Width between outer sides of tritocones of P_4 ..	67	69	65	65
Least width between superior borders of orbits	36 ^{ap}	38.5	39.2	38
Width between postorbital processes of frontals	48 ^{ap}	52 ^{ap}	53.2	55
P_3 , anteroposterior diameter.....	13.1	14	14	13.3
P_4 , anteroposterior diameter.....	22.1	22.8	24 ^{ap}	21.2
P_4 , thickness across protocone.....	8.5	8	8.8 ^{ap}	8.5
M_1 , anteroposterior diameter.....	13	13.8	13.3	13.3
M_1 , greatest transverse diameter.....	17.2	17.8	18.2	16
M_2 , anteroposterior diameter.....	7.7	7.5	6.2	7.3
M_2 , greatest transverse diameter.....	12	12.7	12	10.5
Mandible	2064	1683	1682	11278
Length, anterior end of ramus to middle of posterior side of condyles.....	150 ^{ap}	159 ^{ap}	143 ^{ap}	145.5
Height of mandible below posterior side of P_2	18	19	19.2	17
Height of mandible below posterior side of M_1	25	23.9	22.8	22.5
Thickness of mandible below protoconid of M_1	11	10.8	11.7	11.8
Length from posterior side of \bar{C} to posterior side of M_2	88	90	82	85
P_3 , anteroposterior diameter.....	12.5	12	11.7
P_3 , greatest transverse diameter.....	5.2	4.8	4.8
M_1 , anteroposterior diameter	24.2	23	23.5	22.9
M_1 , greatest transverse diameter of trigonid..	9	9	9.5
M_2 , anteroposterior diameter.....	10	10	10	9.8

^{ap} Indicates approximate measurement.

the McKittrick collection scarcely any intermediate forms between those having the type of M_1 shown by No. 2046 and those possessing a first molar of normal character. However, the collection is small as compared with the approximately 200 skulls in the Museum of Vertebrate Zoology, and

TABLE 7—Measurements (in millimeters) of skull, mandible, and dentition of *Canis latrans orcutti* (*Canis latrans ochropus*-like type)

Skull	McKittrick				Recent	
	2047	2048	2049	2050	651 ^a	0-20 ^b
Length from anterior end of premaxillary to posterior end of condyles.....	188	185	186	192 ^{ap}	192	181
Length from posterior side of C to posterior side of M2..	78	75.5	74	82	80	72
Length from anterior side of P4 to posterior side of M2..	38	39	39	38.7	35.2
Least width of muzzle between C and P4.....	29	30	32.6	32.2	28.5
Width across zygomatic arches	102	98 ^{ap}	104	91
Width between outer sides of tritocones of P4.....	59.5	61	59.2	63	57	55
Least width between superior borders of orbits.....	33.8	38.5	39.5	38	35.4	32
Width between postorbital processes of frontals.....	54 ^{ap}	54 ^{ap}	55	54.7	53.5	45
P3, anteroposterior diameter.	11.2	13	12.5	13.2	13.2
P4, anteroposterior diameter.	20.2	22	21.8	22	20.8
P4, thickness across protocone	7.5	8	8	8.2	7.5
M1, anteroposterior diameter.	13	13	13	13	12.8
M1, greatest transverse diameter	16	16.8	17	17.8	16
M2, anteroposterior diameter.	8	7	7	8
M2, greatest transverse diameter	11.5	10.9	12	11.3
Mandible		2068	2069	2067		
Length, anterior end of ramus to middle of posterior margin of condyles.		143	146 ^{ap}	153 ^{ap}	149
Height of mandible below posterior side of P2.....		17.2	18.2	18	16.3
Height of mandible below posterior side of M1.....		24	22	24	19.4
Thickness of mandible below protoconid of M1.....		10	9.2	11.4	10
Length from posterior side of C to posterior side of M2.....		82	82	84	85
P3, anteroposterior diameter.....		11	12	11.5
P3, greatest transverse diameter.....		5	4.8	4.5
M1, anteroposterior diameter.....		23	22.5	23.3	22.2
M1, greatest transverse diameter of trigonid		9	8.8	9	8.1
M2, anteroposterior diameter.....		11	10	10	9.8

^a Large specimen of *Canis l. ochropus*, M.V.Z., Univ. Calif.^b Small specimen of *Canis l. ochropus*, Calif. Inst. Tech.^{ap} Indicates approximate measurement.

this apparent absence of intermediate types does not seem a valid criterion for subspecific or specific differentiation.

With regard to skull characters, the most marked variation other than size and width of muzzle is seen in the occipital region. In some specimens, as for example No. 2049, a well-marked inion is present; while in others, No. 2046 for example, a noticeable overhang of the occipital crest is not shown. The outlines of the zygomatic arches are also subject to consider-

TABLE 8—Measurements (in millimeters) of skull and mandible of *Ænocyon dirus*

Skull	McKittrick *			Rancho La Brea **	
	2077	2078	2079	U.C. 10856	U.C. 10834
Length from anterior end of premaxillary to posterior end of occipital condyles	282	272	260	282	267
Length from anterior end of premaxillary to anterior end of posterior nasal opening.....	151	146	141	155	141
Width across rostrum measured between outer sides of bases of canines	57	59	58	67.3	58.5
Width measured between outer sides of superior sectorials.....	98	94	99	107.5	96.2
Width across zygomatic arches.....	169	166.5	164	175 ^{ap}	164.5
Least diameter between superior borders of orbits.....	60	57.3	63	64.9	54.1
Width between postorbital processes of frontals.....	78	79	90 ^{ap}	93.9	77
Length from a line drawn between posterior borders of glenoid fossæ to posterior end of occipital condyles	60	58	55	54	57
Mandible					
Length from anterior end of left ramus to middle of condyle.....	224	217	230 ^{ap}	210.5
Height measured between summit of coronoid process and inferior side of angle.....	90 ^{ap}	91.3	87
Height of ramus below hypocond of MI	38	37 ^{ap}	38.5	39.7	35.3
Height of ramus below protocond of P3	36	32.5	35	36.9	32.5
Thickness of ramus below protocond of MI.....	17.5	18 ^{ap}	19	20.3	19.3

* Selected from a series of 7 individuals.

** After Merriam (1912).

^{ap} Indicates approximate measurement.

able variation, and the angle subtended by a line connecting the postorbital processes of the frontals and the superior border of the jugal varies within an arc of from 10° to 15°.

Also referred to *Canis latrans orcutti*, at least tentatively, are two very small although mature mandibular rami, Nos. 2075, 2076. In shortness of tooth-row these elements closely approximate *Canis andersoni*, but the roughened condition of the bone seems to indicate that the specimens were not normally developed.

Ænocyon dirus (Leidy)

The common species of Pleistocene dire or grim wolf is represented in the collections of the California Institute of Technology by four nearly complete skulls, Nos. 2077-2080, Plate 8, figs. 1-2a, numerous mandibular elements, and by various skeletal parts. The structural characters of *A. dirus* are well known, owing particularly to the work of J. C. Merriam, so that it is not deemed necessary to make extended comparisons. As is shown by tables 8 and 9, some individuals equal the larger specimens from Rancho La Brea in nearly all skull measurements, and may actually exceed them in size of the crushing teeth. In all details the McKittrick specimens agree very closely with those from Rancho La Brea.

Ænocyon near milleri (Merriam)

This species was based largely on skull characters. The only diagnostic features of the teeth are that in M₁ the hypocone is unusually large and extends around the antero-internal region of the protocone where it is connected with the cingulum (Merriam, 1912, p. 247). In *Ænocyon dirus* this tooth is somewhat larger than in *milleri*. In addition the hypocone is greatly reduced and does not extend so far anteriorly. *Canis occidentalis furlongi* resembles *Ænocyon milleri* insofar as the general characters of this tooth are concerned (Merriam, 1912, pp. 251-254), but differs in the somewhat smaller size, and, if Merriam's figures are reliable, in shape of the para- and metacones as well. In *Canis o. furlongi* these cusps are rather round, while in *A. milleri* they appear to be divided into four sub-equal quadrants by two almost mutually perpendicular cross ridges. The metaconule also appears to be less well developed in *Ænocyon milleri*.

In the collections of the California Institute of Technology are a right and a left M₁, Nos. 2082, 2083, Plate 8, figs. 3, 4, which according to the above analysis belong to *Ænocyon milleri* rather than to *A. dirus* or to the timber wolf. Since *A. milleri* is rare also at Rancho La Brea, its very scanty representation at McKittrick is not surprising. For measurements of these teeth see table 10.

Vulpes macrotis cf. mutica C. H. Merriam

This species of fox is represented by an incomplete skull, No. 2084 C.I.T., Plate 9, figs. 2, 2a, a fragment of right maxillary, No. 2085 C.I.T., Plate 9, figs. 1, 1a, in addition to several mandibular rami.

The skull is somewhat crushed, and lacks the zygomatic arches and a large part of the premaxillaries and occipital condyles. The only teeth present are P₄ and the molars on the right side. There is no trace of a lyrate temporal crest. This character in conjunction with lack of a pronounced inflection on the postero-inferior border of the horizontal rami definitely exclude the form from the genus *Urocyon*. Other characters of the skull are (1) muzzle long and slender, (2) bullæ deep with very large external auditory meatus, (3) brain-case sharply bulged above external auditory meatus, (4) palate very narrow, (5) postorbital process sharply pointed, recurved, and with but little concavity above, (6) anterior palatal foramina do not extend to rear of canines, and (7) basicranial region between bullæ relatively narrow. These characters, especially the first and fifth, seem to exclude the McKittrick form from the gray foxes. On the other hand the first, second, and fourth characters apparently place No. 2084 in the group of *Vulpes macrotis* or kit foxes.

TABLE 9—Measurements (in millimeters) of dentition of *Ænocyon dirus*

Upper Dentition	McKittrick *			Rancho La Brea **	
	2077	2078	2079	U.C. 10856	U.C. 10834
I3, greatest anteroposterior diameter	11.5	10
C, greatest anteroposterior diameter at upper edge of enamel.....	14	15.5	14.6	17
P1, greatest anteroposterior diameter	10.2	9.4
P2, greatest anteroposterior diameter	15.9	16	16	16.2
P3, greatest anteroposterior diameter	18	17.1	19	18.1
P3, greatest transverse diameter...	7.2	7.5	7.9
P4, greatest anteroposterior diameter	32	31	31	32	30.7
P4, greatest transverse diameter across deutocone.....	15.5	16	14	16.2	15
P4, greatest transverse diameter across protocone.....	12.5	12.4	12	13	13
M1, greatest anteroposterior diameter	18.5	19.8	18.6	20	18.7
M1, greatest transverse diameter...	24.2	24.8	23	24	23
M1, transverse diameter of protocone	12.6	12.1	12.1	13.6
M2, greatest anteroposterior diameter	10	7.8	10	9.2
M2, greatest transverse diameter...	15.2	13	15.4	14.4
Lower Dentition					
C̄, greatest anteroposterior diameter at lower edge of enamel.....	15	15.2	20	17.5
P1, greatest anteroposterior diameter	7.7	7.4
P2, greatest anteroposterior diameter	16.5	14.5	16.2	15.4	15.3
P3, greatest anteroposterior diameter	17.5	17.2	16.7	15.8
P4, greatest anteroposterior diameter	20.1	19.2	21	20	19.5
M1, greatest anteroposterior diameter	37	37.3	35.2	35.7	34.5
M1, greatest transverse diameter of heel	13	13	13	13.5	13
M1, greatest anteroposterior diameter of heel.....	9	8.5	9	9.2	8.8
M1, greatest transverse diameter of trigonid	14.2	13.5	14.2	14.3	13.6
M2, greatest anteroposterior diameter	14.2	13	12.8	13.3
M2, greatest transverse diameter...	10.5	10	10	9.3
M3, greatest anteroposterior diameter	7	6.5	7.3

* Selected from a series of 8 individuals.

** After Merriam (1912).

As is shown by table 11, No. 2084 is considerably larger than *Vulpes macrotis arsipus*. While specimens are not available for comparison, C. Hart Merriam (1902, p. 74) states that *Vulpes macrotis mutica* is large and it seems reasonable to refer the McKittrick form to this race, which still inhabits the San Joaquin Valley.

TABLE 10—Measurements (in millimeters) of dentition of *Ænocyon milleri*

Upper Dentition	McKittrick 2082	Rancho La Brea *		
		U.C. 11257 ^a	U.C. 11283 ^b	U.C. 19792 ^b
M1, greatest anteroposterior diameter....	17.5	16.4	16	17.2
M1, greatest transverse diameter.....	22	20.7	19.3	21.5
M1, transverse diameter of protocone.....	12	12.7

* Measurements after Merriam (1912).

^a Type of *Ænocyon milleri*.

^b *Canis occidentalis furlongi*.

TABLE 11—Measurements (in millimeters) of *Vulpes macrotis* cf. *mutica*

Skull	McKittrick		Recent * HX 27
	2080		
Length from occipital crest to posterior end of canine....	100 ^{ap}	96
Width across postorbital processes of frontals.....	29.7	25.5
Greatest width of parietals.....	42 ^{ap}	42.8
Mandible	2129	2128	
Length from condyles to back of lower canine.....	76.5	73
Depth below M1.....	10.8	10.2	8
Thickness below M1.....	4.5	4.9	4.3
Upper Dentition	2084	2085	
P4, greatest anteroposterior diameter.....	11.2	10.8
M1, greatest anteroposterior diameter.....	7	6.4	6.2
M1, greatest transverse diameter.....	10	9.7	9.4
M2, greatest anteroposterior diameter.....	4.5	3.7	3.5
M2, greatest transverse diameter.....	7.4	6.2	6.2
Lower Dentition		2128	
M1, greatest anteroposterior diameter.....	11.5	11
M2, greatest anteroposterior diameter.....	5.1	5

* A female specimen of *Vulpes macrotis arsipus* from Riverside County, California, in the Dickey Collection.

^{ap} Indicates approximate measurement.

MUSTELIDÆ

The McKittrick mustelids have been studied by E. Raymond Hall. All the types found in the asphalt belong to living species and subspecies although *Mustela frenata nigriauris* no longer inhabits the area. For convenience, Hall's remarks concerning the McKittrick mustelids are given below.

The same author has revised the Rancho La Brea and Carpinteria mustelids (1936, pp. 41-119) and his lists are followed in this paper. Hall's study of the mustelid faunas from the California tar seeps is of interest in that it emphasizes the essential similarity and relatively Recent age of these assemblages.

Mustela frenata nigriauris Hall

Concerning the McKittrick weasel, Dr. Hall makes the following statement:

"The collection of vertebrate fossils at the California Institute of Technology contains a nearly complete skull and lower jaw possibly of the same individual, from one of the excavations made in the asphalt deposits at McKittrick. The subspecies of *Mustela frenata* found in the region of McKittrick today is *Mustela frenata pulchra*. Its skull differs from that of the two coastal subspecies, *M. f. nigriauris* and *M. f. latirostra* in a way which permits satisfactory subspecific identification of the skulls alone.

"The skull from McKittrick, allowing for differences due to its lesser age, is a duplicate of the skull of a Recent adult male, No. 46723, Mus. Vert. Zool., of the coastal subspecies, from five miles southeast of Santa Margarita, San Luis Obispo County. This Recent skull, others from places in the coastal district to the southeast of McKittrick, and the fossil one from McKittrick, are intermediate in structural features between *M. f. latirostra* to the south and *M. f. nigriauris* to the north, though decidedly nearer the latter.

"The skull from McKittrick, then, is of the subspecies *nigriauris* which does not occur in that region today but instead farther to the westward in the more humid coastal area."

Mephitis mephitis holzneri Mearns

In regard to the striped skunk Hall states:

"On October 20, 1932, I found, among material being prepared for study at the California Museum of Palæontology, and not at the time given catalogue numbers, the lower jaw bearing M1 and P4 of a young *Mephitis mephitis* taken from the asphalt deposits at McKittrick. The specimen is not identifiable as to subspecies and is here referred to *holzneri* on geographic grounds."

Spilogale phenax phenax C. H. Merriam

Hall comments on the spotted skunk as follows:

"Two lower jaws of the right side and one of the left, in the collection of vertebrate fossils at the California Institute of Technology from locality 138, an excavation in the asphalt deposits at McKittrick are to me indistinguishable from *S. p. phenax*, the Recent form found also in that region."

Taxidea taxus cf. neglecta Mearns

The following remarks concerning the McKittrick badger are made by Hall:

"The writer has examined specimens from the McKittrick asphalt deposits, which are at present being prepared for study and are not yet provided with catalogue numbers. This material, in the University of California Museum of Palæontology, comprises three skulls, six lower jaws and the larger part of the body skeleton of one individual. In the collection of vertebrate fossils at the California Institute of Technology there are available parts of three skulls and four lower jaws. Comparisons fail to reveal any structural features distinguishing the fossil specimens from ones of the Recent animal found in Kern County."

URSIDÆ

This family is represented in the McKittrick fauna by a species of *Tremarctotherium*, and by a form closely related to the existing black bear. These species are not particularly abundant either at Rancho La Brea or at McKittrick. In its massive size and very heavy molar dentition, the black bear appears distinct from any species previously described and has been designated *Ursus optimus*.¹

In view of the present state of the literature, no one can venture to describe a new species of ursid without misgivings for from the palæontological point of view many characters used in separating living forms are of little value. In dealing with fossil types, it appears expedient to accept the distinctions between grizzly and other types as constant, although these are known to vary in existing species (C. H. Merriam, 1918, p. 13). Moreover, criteria for determining the living forms have not been critically examined except for the recent work of Stovall and Johnston (1935, pp. 212-213) who find many of them to be unreliable. Relative proportions of skulls and teeth furnish perhaps a sound distinction, and a series of thirteen skulls representing three subspecies of existing black bears has been studied in order to determine what the expectable range of variation within a species may be. The results indicate that the McKittrick form, although closely related to existing California black bears, is a species now extinct.

The short-faced bears of McKittrick and Rancho La Brea were referred to the genus *Arctotherium* by Merriam and Stock (1925, pp. 7-9). Kraglievich (1926, pp. 14-16) has since demonstrated that the North American species—*yukonense*, *simum*, and *californicum*—are generically distinct from *Arctotherium latidens*, a South American species which is the genotype. For the North American species this author proposed the new genus *Tremarctotherium*. Matthew (1929, p. 474) arrived independently at the conclusion that *T. simum* is generically distinct from *A. bonerense*, and after seeing Kraglievich's article agreed tentatively that the former is separable as *Tremarctotherium*.

T. californicum as defined by Merriam (1911A, p. 165) differs from *T. simum* principally in its larger size. At a later time Merriam and Stock (1925, p. 9) concluded that the two are at least subspecifically distinct, and until the time relation of Potter Creek Cave to Rancho La Brea is

¹ In commenting on the distinctive characters of this bear, Dr. Stock has suggested that the form may have lived under very nearly ideal or optimum conditions, hence the specific name.

better known the arctotheres from these localities might be regarded as distinct species.

While it is true that most of the McKittrick arctothere material agrees closely in size with *T. simum* from Potter Creek Cave, there is in the collections of the University of California a left M $\bar{2}$, No. 33112, which equals in size the average of *T. californicum* from Rancho La Brea and exceeds even the largest second lower molar of that species in anteroposterior diameter (see table 15). On the other hand, a metatarsal I, No. 12768 U.C., from Rancho La Brea is of nearly the same size as the corresponding element in *T. simum*. In addition, a M $\bar{1}$, No. 2088 C.I.T., bridges the gap between *T. simum* and *T. californicum* (see table 15). Therefore, unless both *T. simum* and *T. californicum* are to be recognized as occurring at McKittrick and Rancho La Brea, it seems necessary to conclude that the latter is synonymous with Cope's species.

TABLE 12—Measurements (in millimeters) of skull of *Tremarctotherium simum*

	McKittrick U.C. 33111	Potter Creek Cave * U.C. 3001
Length, anterior end of premaxillary to inion.....	377	391
Length, anterior end of premaxillary to posterior end of condyle	352
Length, anterior end of premaxillary to inferior notch between condyles.....	331.5
Length, anterior end of premaxillary to anterior border of posterior nasal opening.....	196.5
Length, from posterior end of glenoid cavity to posterior end of condyle.....	111.9
Length, anterior side of premaxillary to posterior side of auditory meatus.....	296	300
Length, from postorbital process of frontal to inion.	226.5	220
Length, from anterior border of orbit to posterior side of auditory meatus.....	195.8	192
Length, from anterior border of premaxillary to anterior side of orbit.....	110
Greatest width across muzzle from outer walls of canine alveoli	96.7	101.5
Width across frontal at narrowest point between orbits	116.3	112
Greatest width across postorbital processes.....	152 ^{ap}	150 ^{ap}
Least width of postorbital constriction.....	100 ^{ap}
Greatest width across zygomatic arches.....
Greatest width across mastoid processes.....	167 ^{ap}
Greatest diameter across condyles.....	73.3
Palate, width between middle internal borders of M $\bar{1}$	73	80
Width of nasals anteriorly.....	47
Length of nasals.....	85.2	81
Width of anterior nares.....	74.4	77
Height of anterior nares.....	70	63
Height of orbit.....	56	50
Height, inferior border of maxillary to top of frontal between postorbital processes of frontal.....	136	121
Height of inion above superior border of auditory meatus	96	94
Height of inion above base of occipital condyles.....	116

* Measurements of Potter Creek Cave material after Merriam and Stock (1925).

^{ap} Indicates approximate measurement.

It is possible that *T. californicum* is a subspecies of *T. simum*, but since subspecies are based on lateral rather than vertical distribution, this does not seem to be probable. However, during the Pleistocene there may have been considerable shifting of ranges of subspecies, but in the present instance this still awaits demonstration.

***Tremarctotherium simum* (Cope)**

The McKittrick collections of the University of California contain a nearly complete skull, No. 33111, Plate 10, figs. 1-1b, and mandible, No. 33111, Plate 10, fig. 2, of this species. These specimens probably belong to the same individual, for the teeth appear to be in the same stage of wear in both the upper and lower jaws. The skull is that of an old individual, for the sutures are closed and the teeth rather deeply worn.

As is shown by table 12, the skull is slightly smaller in nearly all measurements than *T. simum* from Potter Creek Cave. The teeth, on the other hand, usually equal and often exceed the dimensions of comparable teeth in the cave material (see table 13). In all details, the tooth pattern closely

TABLE 13—Measurements (in millimeters) of upper dentition of
Tremarctotherium simum

	McKittrick U.C. 33111	Potter Creek Cave *	
		U.C. 3001	U. C. 3005
Greatest transverse diameter of incisor series, measured at cingulum of I ₃		57.2
Length from anterior side of C to posterior side of M ₂	140.3	136.8
Length from anterior side of P ₄ to posterior side of M ₂	77.6	76
I ₁ , greatest transverse diameter.....		7.9
I ₂ , greatest transverse diameter.....	10.1	9
I ₃ , greatest transverse diameter.....	10.6	10.8
C, anteroposterior diameter at base of enamel.	28.5	27.9
P ₁ , greatest anteroposterior diameter.....		10.4
P ₂ , greatest anteroposterior diameter.....	
P ₃ , greatest anteroposterior diameter.....	8.3	8.5
P ₃ , greatest transverse diameter.....	5	5
P ₄ , greatest anteroposterior diameter.....	21	20.5	20.4
P ₄ , transverse diameter across protocone.....	15	15	15.3
M ₁ , greatest anteroposterior diameter.....	23.5	24	23.8
M ₁ , greatest transverse diameter.....	22.5	23	22.1
M ₂ , greatest anteroposterior diameter.....	33.9	35	33
M ₂ , greatest transverse diameter.....	22.2	22	21.4

* Measurements of Potter Creek Cave material after Merriam and Stock (1925).

approximates that in the cave material. Owing probably to injury, the posterior portion of the frontal region is deeply indented, and this may be responsible for the more pronounced bulge in the contour of the skull above the orbits of the McKittrick specimen than is seen in *T. simum* from the northern California cave. The middle, posterior incisive foramen is almost as large as either of the anterior two, and is much larger than the correspond-

ing opening in U.C. No. 3001 from Potter Creek. Two infraorbital foramina are present on each side of the skull.

The mandible is similar to that of *T. simum* from Potter Creek, but in the McKittrick specimen the space between the third and fourth lower premolars is somewhat greater than in a specimen from the former locality, U.C. No. 3004.

A single left M $\overline{2}$, No. 33112 U.C., is remarkable for its large size. As is shown by table 15, this tooth exceeds even the largest comparable tooth from Rancho La Brea in anteroposterior diameter.

TABLE 14—Measurements (in millimeters) of mandible of *Tremarctotherium simum*

	McKittrick U.C. 33111	Potter Creek Cave U.C. 3001 *
Length from posterior side of condyle to anterior alveolar border	252	262
Height at anterior end of M $\overline{1}$	51	58.5
Height at anterior end of M $\overline{3}$	65.5	75.4
Thickness below posterior end of M $\overline{1}$	24.2	25.5

* After Merriam and Stock (1925).

TABLE 15—Measurements (in millimeters) of lower dentition of *Tremarctotherium simum*

	McKittrick U.C. 33111		Potter Creek Cave U.C. 3004	
C, greatest anteroposterior diameter at base of enamel.....	24.3
P $\overline{4}$, greatest anteroposterior diameter.	11.6
P $\overline{4}$, greatest transverse diameter.....	7
M $\overline{1}$, greatest anteroposterior diameter	29.7	34 *	30.5	35 **
M $\overline{1}$, transverse diameter across protoconid	14.5	14.3 *	14.4	16.6 **
M $\overline{1}$, width of heel.....	16.8	17 *	18 **
M $\overline{2}$, greatest anteroposterior diameter	25.5	33.3 ***	27.2	31.7 **
M $\overline{2}$, transverse diameter across protoconid	18.7	21.8 ***	19.8	22.4 **
M $\overline{3}$ greatest anteroposterior diameter.	18.8	19.7
M $\overline{3}$, transverse diameter across protoconid	14.9	16

* C.I.T. No. 2088 from McKittrick.

** L.A. Mus. No. Z6 from Rancho La Brea.

*** U.C. No. 33112 from McKittrick.

The material in the collections of the California Institute of Technology consists of a canine tooth, No. 2087, an M $\overline{1}$ from the right side, No. 2088, and numerous more or less complete appendicular and axial skeletal elements.

All are nearer in size to specimens from Potter Creek Cave than to those from Rancho La Brea. Certain elements, ulna No. 2089 for example, are even smaller than corresponding parts of the Potter Creek form. On the

TABLE 16—Measurements (in millimeters) of appendicular skeleton of *Tremarctotherium simum*

Metacarpal IV	McKittrick	Potter Creek Cave **
	2096	U.C. 3040
Greatest length	119.5	106.2
Anteroposterior diameter of proximal end.....	27.5	31
Least width of shaft.....	15	15.8
Greatest width of distal end.....	23.5	25.7
Metacarpal V	2097	104 32.3 16.1 25.5
Greatest length	98	
Anteroposterior diameter of proximal end.....	28	
Least width of shaft.....	14	
Greatest width of distal end.....	23	
Metatarsal III	2098	
Greatest length	108	
Anteroposterior diameter of proximal end.....	33	
Least width of shaft.....	15.7	
Greatest width of distal end.....	24.4	
Metatarsal IV	2099	
Greatest length	122	
Anteroposterior diameter of proximal end.....	31.5	
Least width of shaft.....	15.8	
Greatest width of distal end.....	25.5	
Calcaneum	2100	L.A.M. 10214
Greatest length (a-axis)*.....	103.5	110
Greatest width measured obliquely across sustentaculum (b-axis)*	72	77.8
Width of cuboid facet (c-axis)*.....	38.5	39.4
Unciform	43.7	U.C. 24067
Proximo-distal diameter (a-axis)*.....	28	47.6
Anteroposterior diameter of distal articulating surface (b-axis)*	27	34.7
Transverse diameter of distal end (c-axis)*.....		36.5

* For explanation of system of axes see Merriam and Stock (1925, pp. 26, 31).

** Measurements of Potter Creek Cave material after Merriam and Stock (1925).

other hand, MĪ equals the larger individuals from Rancho La Brea in anteroposterior diameter but in transverse measurement more nearly approximates the cave material.

Ursus optimus n. sp.

Type Specimen.—Skull No. 2090 C.I.T., Plate 11, figs. 1-1b. This specimen presumably represents a rather old male and is complete except for the incisor and premolar teeth, the occipital condyles, and the outer portions of the zygomatic arches.

Cotype.—A mandible No. 2091 C.I.T., Plate 11, fig. 2. This specimen lacks only the incisors, the first two premolars, and the coronoid process on the right side.

Referred Material.—A right and a left M $\bar{2}$, Nos. 2093, 2094; part of a palate with molar teeth, No. 2092; a left and a right femur, a left and a right humerus, tibia, ulna, ilium, in addition to various metapodials and rib and vertebral elements. All specimens are in the collections of the California Institute.

Specific Characters.—Skull very wide in relation to its length. Mandible heavy, the horizontal rami being very thick and deep below the diastema and lower cheek-teeth. Upper and lower molars very large, premolars relatively reduced in size.

Skull and Mandible.—Although the occipital crest and condyles are somewhat damaged, it is apparent that overhang of the inion is less pronounced in the Pleistocene species than in the living black bear. Other than this there is little difference between the skull profiles of the two. In both instances the anterior half of the nasals projects nearly straight forward. The frontals are arched and the apex is located slightly in front of the fronto-parietal suture. *Ursus optimus* is relatively broader in nearly all skull proportions than the living species, *Ursus americanus*, and this is especially true for the muzzle. The one exception is the posterior nares, which are relatively narrower than in the latter. In the fossil skull the postpalatine and sphenopalatine foramina are located in an elongated depression, or sulcus, a feature not seen in any of the Recent skulls examined. In all other respects the McKittrick species is very similar to the living black bear.

Except for its massive appearance and greater depth, the mandible offers little to distinguish it from *Ursus americanus*. The symphyseal region is relatively wider, however, and the horizontal rami are somewhat deeper below the diastema and lower cheek-teeth. The condyles are also a little heavier and wider than are commonly seen in the living form. As in the latter, the coronoid flange is long and only moderately produced posteriorly, while the masseteric fossa is wide and very deep. The inferior border of the horizontal ramus is straight in both the living and fossil forms.

Dentition.—The dental formula is $\frac{3}{3} \frac{1}{1} \frac{3}{3} \frac{2}{3}$. In *Ursus americanus* the third lower premolar is occasionally lacking. It is probable, however, that a similar tooth reduction may be found in individuals of the Pleistocene species, for in the latter P $\bar{3}$ is very small. Spacing of individual teeth is very similar to that of the modern species, except that the diastema between the third and fourth lower premolars appears to be somewhat longer in the fossil form.

Alveoli for the upper incisors indicate that the first two teeth were subequal in size, while the third must have been very much larger than either of the two inner incisors. The upper canines are very large and curved as in the modern form. The second upper premolar is somewhat larger than P $\bar{3}$, but neither tooth is more than a mere peg. P $\bar{4}$ is broken off at the roots and all that can be said is that this tooth was probably triangular in

TABLE 17—Measurements (in millimeters) of skull and mandible of *Ursus optimus*

Skull	McKittrick 2090	M.V.Z., Univ. of Calif.*		
		20746♂? ^a	16375♂? ^b	4678♂? ^c
Length from anterior end of premaxillary to posterior end of condyles	330 ^{ap}	309	291	274
Length from anterior end of premaxillary to posterior end ofinion. Length of palate from anterior end of premaxillary to a line tangent to posterior surfaces of maxillary parapets	336 ^{ap}	324	313	298
Length from posterior end of glenoid cavity to posterior end of condyles. Length from anterior end of premaxillary to anterior end of posterior nasal opening.....	142	138	132	127
Anteroposterior diameter of nasals... Width of anterior nares.....	111 ^{ap}	96	93	90
Breadth of rostrum immediately posterior to roots of upper canines.... Least width between superior borders of orbits.....	158	163	145	149
Width across postorbital processes.... Least width of postorbital constriction	88 ^{ap}	92	85	77
Greatest width across zygomatic arches	42	41.6	32.5	34.4
Anterior palatal width between superior canines.....	84.2	71	65	60
Posterior palatal width between posterior borders of M2.....	90	79	80.5	73
	122 ^{ap}	113	114	104
	78	70	72.5	71
	213 ^{ap}	201	200	180
	51	40.2	40	37.5
	51.2	51	48.8	42.5
Mandible				
Length from anterior end of symphysis to posterior end of condyle.....	226	222	193.5
Length of symphysis measured along anterior border.....	73 ^{ap}	64.2	61.5
Least depth of ramus below diastema. Depth of ramus below posterior end of M1.....	41	35	34
Thickness of ramus below M1.....	44.8	37.5	37
Height from inferior border of angle to summit of coronoid process.....	21.2	18	15.1
Transverse width of condyle.....	104.3	91.5	81
Greatest depth of condyle.....	53	47	41.3
Greatest width of mandible measured across symphysis and between outer walls of alveoli for lower canines..	18	15.2	14
	46.2	40	40

* Recent specimens selected in order to show extremes in variation in a series of thirteen individuals:

^a *Ursus americanus altifrontalis*, Trinity Co., California.

^b *Ursus americanus californiensis*, Tulare Co., California.

^c *Ursus americanus altifrontalis*, Eugene City, Oregon.

^{ap} Approximate measurement.

TABLE 18—Measurements (in millimeters) of dentition of *Ursus optimus*

Upper Dentition *	McKittrick	M.V.Z., Univ. of Calif.			
	2090	16375 ^a	29803 ^b	4678 ^c	20746 ^d
Length of upper tooth row from anterior margin of <u>C</u> to back of <u>M2</u>	124.3	108.2	101.5	104	104
<u>C</u> , greatest anteroposterior diameter.....	24.8	19.8	21.2	20.6	22.7
<u>C</u> , greatest transverse diameter	15.7	13	12.3	13	15.1
<u>M1</u> , greatest anteroposterior diameter.....	20.2	17	16.8	17	18
<u>M1</u> , greatest transverse diameter	15	13	12.3	13	13
<u>M2</u> , greatest anteroposterior diameter.....	33.1	26.7	26.5	26	28.2
<u>M2</u> , greatest transverse diameter	17	15	15	14	15.8
Lower Dentition	2091				
Length of lower tooth row from anterior margin of <u>C</u> to back of <u>M3</u>	139	125	118	118.5
<u>C</u> , greatest anteroposterior diameter	23.2	19.8	18	19.8
<u>C</u> , greatest transverse diameter	15	13	12	11.6
<u>P4</u> , greatest anteroposterior diameter	10	10	9.2	10
<u>P4</u> , greatest transverse diameter	6	5.3	5.1	5.1
<u>M1</u> , greatest anteroposterior diameter	21.2	17.4	17	17.4
<u>M1</u> , greatest transverse diameter	11	9	8	9
<u>M2</u> , greatest anteroposterior diameter	22.5	20	19	18.5
<u>M2</u> , greatest transverse diameter	13.8	11.5	11.2	11
<u>M3</u> , greatest anteroposterior diameter	17.2	15.2	14.2	14.5
<u>M3</u> , greatest transverse diameter	14.5	12.8	12	11.8

* Grinnell found that in a series of 13 specimens of California black bears, M2 varies in anteroposterior diameter from a minimum of 23.7 mm. to a maximum of 29.1 mm., while M1 varies in the same measurement from a minimum of 14.5 mm. to a maximum of 18.2 mm.

^a *Ursus americanus*, south fork of Kern River, Tulare Co., California.

^b *Ursus americanus*, Tuolumne Co., California.

^c *Ursus americanus*, Eugene City, Oregon.

^d *Ursus americanus altifrontalis*, California.

shape, as is the case with living black bears. The first upper molar is similar to the corresponding tooth in *Ursus americanus* but is larger. This is true for the last upper molar as well.

The lower incisor alveoli indicate the same relative proportions for these teeth as has been noted for the upper incisors. P $\bar{2}$ and P $\bar{3}$ are very small and the third premolar is practically rudimentary. P $\bar{4}$ although small is nearly of same size as the comparable tooth in the modern black bear and possesses the same conical shape. All three lower molars are similar to those of *Ursus americanus* but are much larger. This discrepancy in size between the molar and premolar series as contrasted with the living form furnishes, perhaps, the most important distinction between the two species. In this connection see table 18.

Skeleton.—The elements at hand furnish little information other than that the body was also large in size. Femur No. 2095 measures 390 millimeters from head to rotular groove. As in *Ursus floridanus* and a fossil specimen from the Conard Fissure referred to *Ursus americanus* (Brown, 1908, p. 184), the deltoid ridge extends far down the shaft of the humerus. Similarly as in *U. americanus*, the ulna shows a very large articular surface for the radius. Metacarpals III and IV measure 72 and 83 millimeters respectively in their longest dimension.

Ursid material from Samwel Cave in the collections of the University of California, namely a skull, No. 8851, and a mandible, No. 1009, seems referable to the new species. The material from Rancho La Brea in the Los Angeles Museum consisting of an immature skull and mandible of a single individual, No. 5500-1, is also referred to *U. optimus*.

Comparisons.—A number of fossil bears have been described from the Pleistocene but usually without specific designation. It is possible that some of these forms are identical with the McKittrick species.

Ursus vitabilis Gidley (1913, p. 96) from a cave deposit near Cumberland, Maryland, differs from *Ursus optimus* in the smaller size of the referred upper molars. The type mandible figured, indicates that in the Maryland form the first three lower premolars have been lost. Otherwise there is little to distinguish the two, except that the molars, M $\bar{1}$ especially, are considerably smaller in the Maryland type.

Ursus procerus Hay (1911, p. 772) differs from the McKittrick species in its more slender skull proportions and in narrowness across the zygomatic arches. Other differences are: the less highly arched frontals and the more slender canines exhibited by Hay's species.

Ursus amplidens Leidy (1853, p. 303) from Natchez, Mississippi, is based on two lower molar teeth. Although the teeth are large, the jaw fragment containing them is considerably more slender than in *Ursus optimus*.

Ursus horribilis oklahomaensis Stovall and Johnston (1935, pp. 208-213) from the Oklahoma Pleistocene agrees somewhat closely with the California specimen in tooth measurements, but differs decidedly in the much more pronouncedinion. Furthermore, the Oklahoma specimen is described as belonging to the grizzly type from which the McKittrick form is distinguished by its more massive skull and conical shape of P $\bar{4}$.

MEGATHERIIDÆ

Ground sloths of this family are not abundant in the McKittrick collection and are represented by only one individual of the genus *Megalonyx*. Absence of *Nothrotherium* is peculiar and reasons for this absence are not apparent.

Megalonyx? sp. indet.

A single phalanx II, No. 2101 C.I.T., is referred to this genus. This element corresponds closely in measurements and in general shape to the comparable phalanx of *Myiodon*, but the groove between the distal condyles seems to be too deep for that genus. The phalanx is clearly not that of

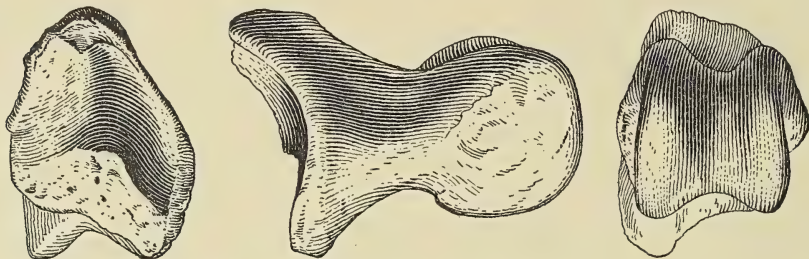


FIG. 7—*Megalonyx?* sp. Phalanx II, C.I.T. No. 2101, proximal, lateral, and distal views. Approx. $\times 2/3$.

Nothrotherium, for both in size and shape there is little correspondence between the two. In *Nothrotherium* the proximal end is subquadrate in outline while in the McKittrick specimen the proximal end is nearly triangular in shape. Since No. 2101 does not correspond to either of the better known genera of ground sloths found at Rancho La Brea, it is referred to *Megalonyx*, the form to which it bears closest resemblance.

MYLODONTIDÆ

Since Stock's (1925) work on the ground sloths of Rancho La Brea, Kraglievich (1928) has demonstrated that *Myiodon darwini* Owen is the type of the genus *Myiodon*, and not *Myiodon harlani* Owen as is the usually accepted view. Kraglievich's illustrations show the former to be characterized by a beak-like premaxillary region and it would seem that this form cannot belong to the same genus as the Rancho La Brea mylodonts. Kraglievich applies the generic name *Paramyiodon* Brown to the asphalt species. Although the latter genus was described on invalid grounds, in consequence of Kraglievich's redefinition *Paramyiodon* becomes a valid name.

Paramyiodon harlani (Owen)

Material in the collections of the University of California consists of several detached teeth, Nos. 33104-33109; a fragment of right maxillary of an immature individual, No. 33110; a left mandibular ramus, No. 33103, also of an immature individual; an ungual phalanx, digit III, of the left manus, No. 33121, and numerous skeletal elements in addition to a large number of dermal ossicles. The material in the collections of the California Institute of Technology consists of dermal ossicles and a few isolated teeth.

All of the teeth show marked resemblance to the Rancho La Brea material. As in the latter (Stock, 1925, p. 128), the external surface of the hard dentine layer is marked by transverse undulating lines, while the external surface of the cement is marked by longitudinal striations. The outlines of the enamel patterns fall within the range of variation of corresponding teeth from Rancho La Brea.

The fragment of immature right maxillary, U.C. No. 33110, contains the last four superior teeth. Although this specimen is considerably smaller than No. 1717-35 from Rancho La Brea (Stock, 1925, fig. 61), the McKittrick specimen is remarkably similar in all other respects to the Rancho La Brea material.

The immature left mandibular ramus, U.C. No. 33103, is of some interest in that it seems to be one of the few young specimens of its kind on record. Judging from Stock's (1925, pp. 127-128) summary of the characters of *Paramylodon harlani* very little change apparently takes place in this element during growth. In both mature and young specimens the horizontal ramus is thick. The depth of the ramus decreases slightly from the base of the coronoid process to the anterior side of the first lower tooth.

In mandible, No. 33103, two mental foramina are present, the lower one of which is the larger. This is also the case with mature specimens, although occasionally more than two openings may be present in this region.

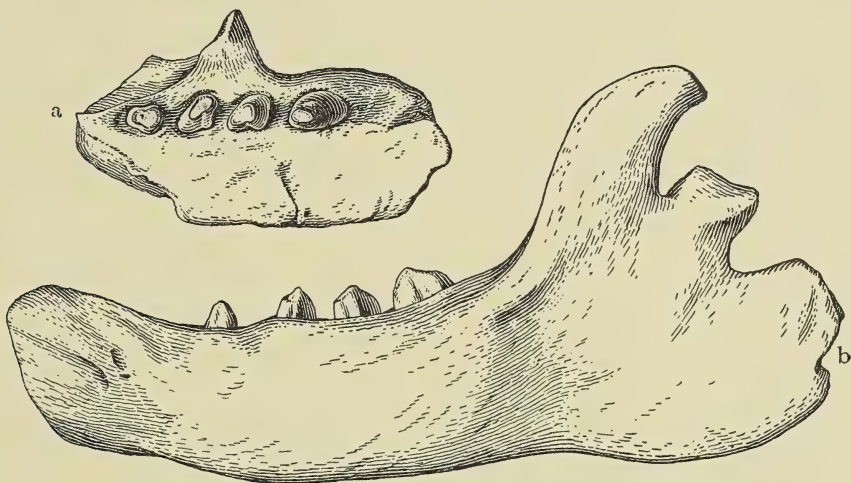


FIG. 8—*Paramylodon harlani* (Owen), immature specimens. a, right maxillary, U.C. No. 33110, occlusal view; b, left mandibular ramus, U.C. No. 33103, lateral view. Approx. $\times 2/3$.

The postero-external opening of the dental canal is situated opposite the posterior lobe of the last lower tooth. Similarly as in mature specimens, the coronoid process slopes slightly backward, and the posterior end of the process extends to a point vertically above the anterior portion of the condyle.

Phalanx, U.C. No. 33121, has lost most of the bony sheath which covers the claw process, but in all other respects resembles the terminal phalanx of digit III of the left manus of *Paramylodon harlani* from Rancho La Brea.

CAMELIDÆ

A monograph of the Rancho La Brea camels by Dr. Stock is in course of preparation and as one of the McKittrick forms is apparently specifically identical with *Camelops hesternus* from the former locality, it is to be expected that any revision of the Rancho La Brea forms will involve a change in status of the forms from McKittrick. In addition to *Camelops*, the

McKittrick assemblage contains the type of *Tanupolama stevensi*. Absence of this genus in the Rancho La Brea fauna raises a puzzling question, which is treated on page 153.

Tanupolama stevensi (Merriam and Stock)

Rather fragmentary remains of this form were first described as *Lama stevensi* by Merriam and Stock (1925A, pp. 39-42). Further study of better preserved material convinced the latter author that the form is generically distinct, although related to the South American llamas (1928A, pp. 29-37).

TABLE 19—Measurements (in millimeters) of *Paramylodon harlani*

Mandible *	McKittrick	Rancho La Brea **
	U.C. 33103	
Length from anterior end of symphysis to posterior end of condyle	153
Greatest length of symphysis.....	41.5 ^{ap}
Greatest pre-dental width.....	57 ^{ap}
Depth of ramus between third and fourth inferior teeth, measured normal to inferior margin.....	34.9
Maxillary *	U.C. 33110	
Greatest length of upper tooth row.....	57
Dentition		U.C. 21158
2, anteroposterior diameter.....	26	28.8
2, transverse diameter.....	14	20.7
4, anteroposterior diameter	25.5	25.5
4, transverse diameter.....	21.6	27.8
		L.A.M. 1717-2
5, anteroposterior diameter.....	23.2	23
5, transverse diameter.....	18	19.3

* Immature specimen.

** All measurements of Rancho La Brea material after Stock (1925, table 64).

^{ap} Approximate measurement.

The type specimen is a fragmentary mandible in the collections of the University of California, U.C. No. 24260. The generic characters are as follows:

Size of average specimens larger than living llama, but smaller than *Camelops*.

Orbits smaller, brain-case larger and somewhat flatter dorsally than in *Lama*.

Posterior portion of mastoid region and paroccipital process situated closer to basioccipital and occipital condyles than in living genus. Deep narrow groove on postero-external side of mastoid behind stylo-hyal pit.

Paroccipital process bluntly pointed and not projecting inward in its downward course.

Lower canine present or absent. Lower molars with inner enamel surfaces flatter and median longitudinal groove of inner side not as deep as in *Lama*. Antero-external style not as well developed as in living genus. Posterior lobe of $M\bar{3}$ wider transversely and less prominently constricted from second lobe.

Limb elements much more slender than those of *Camelops*. Radius-ulna and cannon bones greatly elongated. Metapodials in some individuals approaching those of *Camelops hesternus* in length.

NOTES ON THE MILK-DENTITION OF *TANUPOLAMA STEVENSI*

Since Stock's original description, an excellent series illustrating the milk-dentition of this form has become available at the University of California. This institution also possesses a representative collection of milk-teeth of *Procamelus* and *Pliauchenia*. Opportunity is taken, therefore, to supplement knowledge of the slender-limbed Pleistocene camel by a comparison of milk-dentitions of this and the Tertiary forms.

In the lower jaw of *Tanupolama* two milk-teeth are present, $Dm\bar{3}$ and $Dm\bar{4}$. The former is small, and possesses two lobes. $Dm\bar{4}$ is larger and shows three well defined lobes. In some specimens, U.C. No. 33114, for example, the outer valleys between the lobes carry well defined pillars; while in others, U.C. No. 33114a, no trace of pillars can be seen. A fragment of left maxillary, U.C. No. 33114b, contains $Dm\bar{2}$ and $Dm\bar{3}$, but four deciduous upper molars are present in C.I.T. No. 31.

In *Procamelus* material of the University of California from Burge and Gordon Creek, Nebraska, $Dm\bar{2}$ is always present. In addition, $Dm\bar{3}$ is somewhat larger than the corresponding tooth of *Tanupolama*, and shows definite indications of three lobes. $Dm\bar{3}$ is much alike in both genera, except that in *Procamelus* the external buttresses seem to be invariably absent.

In the upper deciduous dentitions there seems to be little difference between the Pleistocene and Pliocene genera except that in *Tanupolama* $Dm\bar{2}$ is greatly reduced in size as compared with the same tooth in *Procamelus*. In the latter genus this tooth is long and narrow and possesses three lobes while in *Tanupolama* $Dm\bar{2}$ is very small and shows no tendency to develop lobes. In addition, the long axis of this tooth describes an angle of approximately 45° with the rest of the tooth-row, while in *Procamelus* $Dm\bar{2}$ is parallel in its long dimension with the tooth-row.

The collection of milk-dentitions of *Pliauchenia* from Hemphill, Texas, now in the collections of the University of California offers good comparative material. The milk-teeth of this form are distinguished from corresponding teeth of *Tanupolama* by the following characters:

In *Pliauchenia* $Dm\bar{2}$ is always present, but while in some instances as for example in U.C. No. 30886 this tooth is closely appressed to $Dm\bar{3}$, in other cases, U.C. No. 30888, an interval of approximately one centimeter separates $Dm\bar{2}$ from $Dm\bar{3}$. This may indicate that in *Pliauchenia* the second lower milk-molar was in process of suppression. As in *Procamelus*, $Dm\bar{3}$ of *Pliauchenia* is a three-lobed tooth, but the first lobe is often quite obscure. Similarly, as in *Procamelus* and in contrast to *Tanupolama*, $Dm\bar{4}$ of *Pliauchenia*, although three-lobed, never shows the presence of pillars on the external valleys between the lobes.

In the upper milk-molars of *Pliauchenia* $Dm\bar{2}$ is more reduced in size than in *Procamelus*, but somewhat less so than in *Tanupolama*. In con-

trast to the latter and as in *Procamelus*, the long axis of this tooth is parallel to the tooth-row instead of describing an angle to that plane. For complete measurements of *Tanupolama* the work of Stock (1928A) should be consulted.

Camelops hesternus (Leidy)

Remains of this camel from the McKittrick deposits include various cranial, axial, and appendicular elements.

Skull and Permanent Dentition.—The single mature cranial element available, C.I.T. No. 2102, consists of the maxillaries and a complete cheek-tooth dentition. The skull is approximately intermediate in size between Nos. 20028 and 20040 in the University of California collections from Rancho La Brea.

The teeth are moderately worn and, although departing somewhat from the dimensions of the Rancho La Brea specimens, closely resemble them in shape and outline of the enamel pattern. In both instances P₃ has a narrow and rather blade-like crown, while P₄ is nearly quadrate in cross-section. In M₂ the anterior lobe is noticeably wider than the posterior lobe, while in M₃, as in U.C. No. 20028 from Rancho La Brea, the meta-style is drawn out posteriorly into a wing-like projection.

A single permanent lower molar, C.I.T. No. 2103, because of its relatively narrow transverse diameter is thought to correspond to M₃. However, the one diagnostic feature of M₃ cannot be seen, for the posterior lobe is lacking. All that can be said definitely is that there is no evidence of an antero-external buttress while the inner ribs are very poorly developed.

Skeletal Elements.—These consist of numerous vertebræ and limb and foot elements. All are of large size. The metapodials in particular are very heavy and are readily distinguishable on this character from corresponding elements of *Tanupolama*.

BOVIDÆ

In addition to *Bison antiquus*, which is common to both McKittrick and Rancho La Brea, the former locality has furnished remains of a musk-ox-like animal as yet unknown from the Los Angeles occurrence. This form has been tentatively referred to *Preptoceras* by Stock and Furlong (1927, pp. 409-434), but it was recognized that in many ways the McKittrick form approaches *Euceratherium* while in some characters it resembles neither. The present study has brought to light some additional material representing this interesting form, but not enough to fix its generic reference with any greater degree of certainty.

Preptoceras? cf. *sinclairi* Furlong

The material described by Stock and Furlong consists of a fairly complete skull and mandible, in addition to various limb and foot elements. The following résumé of characters was given by these authors:

Characters like those of Preptoceras.—Size and shape and presumably curvature of horn-core; extent to which horn-core extends outward and backward from the base before curving forward; width across frontals between outer lower borders of horn-cores; indentation of palatine on each side of posterior notch; absence of median ridge on occiput above foramen magnum and general appearance of occiput; parietals form dorsoposterior roof of skull.

Characters like those of Euceratherium.—Backward and upward extent of horn-cores; some resemblance possibly in curvature; width of palate; absence of accessory style in upper molars.

Characters common to Preptoceras and Euceratherium.—Width of frontals between orbital rims; presence of a lachrymal depression; shape of elements and position of foramina in basicranial region of skull; position and size of occipital condyle; number and structure of teeth; structure of feet.

Characters distinguishing the McKittrick form from both Preptoceras and Euceratherium.—Width measured between inner borders of horn-cores; elevation of frontals in their extent from the fronto-nasal suture to horn-cores; depth of lachrymal depression; abrupt downward descent of posterior border of alisphenoid; angle (139°) in vertical plane made by plane of dorsal surface of the cranial roof with plane of the occiput.

It was concluded that of the characters exhibited by the McKittrick form, those allying it with both *Preptoceras* and *Euceratherium* are of greater significance than those which relate it to either of the two genera. It would thus appear that *Preptoceras* and *Euceratherium* are generically identical. If so, the name *Euceratherium* takes precedence over *Preptoceras*. Stock and Furlong suggested that the type of *Preptoceras* may possibly represent a young male and the type of *Euceratherium* an older female.

New material available consists of a very imperfect skull of an immature individual, C.I.T. No. 2106, a very fragmentary left mandibular ramus, C.I.T. No. 2107, also of an immature individual, a right and left third metacarpal, C.I.T. Nos. 2108, 2109, the first and second phalanges IV, C.I.T. Nos. 2110, 2111, and in addition numerous upper and lower milk-teeth.

The milk-dentition consists of three upper and lower premolars. Dp $\bar{2}$ is poorly preserved, but appears to taper toward the front. Dp $\bar{4}$, No. 2113, is likewise very imperfect. There are indications, however, that this tooth was tri-lobed. In addition, it shows two subsidiary cuspules, one on the posterior margin of the valley between the first and second lobes, the other on the anterior border of the posterior valley. The upper milk-teeth show few features of interest. Dp $\bar{2}$ is not present in any of the maxillaries, but from the size and shape of the alveolus, it is inferred that this tooth was very small and quadrate in cross-section.

The skull, No. 2106, contains only the molar teeth on the right side. These correspond very closely to the measurements of No. 27118 U.C. from McKittrick. In all other respects the skull and teeth agree very well with that specimen.

Since only elements of the pes were available at the time of the original description of the McKittrick material, the elements of the fore-feet now at hand are of some importance. The two third metacarpals, Nos. 2108, 2109, although nearly of same length as the corresponding elements of the pes, are considerably broader. This is also true for the proximal and middle phalanges.

Bison antiquus Leidy

This species is well represented in the collections of the University of California and California Institute of Technology. A well preserved skull, No. 2124 C.I.T., is complete except for the tips of the horn-cores, and the fragmentary state of the teeth. It furnishes an adequate basis for reference of the McKittrick bison to *B. antiquus*.

This specimen apparently represents an old male for the horn-cores are quite robust and the neck of the horn-core, i.e., the portion between the forehead and the rugose horn-covered portion, is of smaller caliber than the base of the horn-core itself. According to Chandler (1916A, pp. 126-127), these are distinguishing marks of the male of *Bison antiquus*. As is shown by table 20, the McKittrick skull is considerably larger than most specimens of *Bison antiquus* from Rancho La Brea, but the proportions are so similar as to leave little doubt that No. 2124 is correctly referred to that species.



FIG. 9—*Bison antiquus* Leidy. Skull, C.I.T. No. 2124, dorsal view. Approx. $\times 1/8$.

As in the specimen figured by Chandler (1916A, p. 127, figs. 1a, 1b), the horn-cores curve upward and slightly forward. The angle between the median plane of the skull and horn-cores approximates 90° , and according to Chandler (*op. cit.*, p. 130) this distinguishes *B. antiquus* from *B. bison*. In the latter species this angle varies from 110° to 125° .

The naso-frontal suture is obscured by tar, but as in *B. antiquus* the nasal bones are relatively short and broad, only moderately arched, and taper gradually toward the tip. The teeth are too fragmentary to furnish any evidence of systematic value.

Several fragmentary lower jaws are available. All seem to approximate closely in outline the comparable element of *B. antiquus*. The teeth also show no major differences from those in the latter species.

CERVIDÆ

During excavation of the fossil material a considerable number of deer and elk bones were encountered but principally in the upper and presumably sub-Recent levels of the asphalt. Closer inspection of the material, however, indicates that while most of the cervid remains show the glossy

black appearance characteristic of specimens preserved in Recent tar seeps, a number of elements approximate in their state of preservation the Pleistocene remains. It is inferred, therefore, that members of this family formed a part of the Pleistocene fauna of the area.

Cervus sp.

Two fragmentary metapodials, several astragali, a left unciform, and two right cuneiforms constitute the representation of this form. All of these elements approximate the Tulare elk, *Cervus nannodes*, in size but minor discrepancies in size and shape of the various facets occur between

TABLE 20—Measurements (in millimeters) of skull of *Bison antiquus*

	McKittrick 2124	Rancho La Brea	
		U.C. 21154 *	U.C. 21185 *
Length from lower border of foramen magnum to rear of nasals.....	280	285	290
Length from occipital crest to fronto-nasal suture measured along median line.....	255	272	226
Length from rear of condyles to tip of premaxillaries	440	440 ^{ap}
Length from lower border of foramen magnum to rear of hard palate.....	214
Length from rear of hard palate to tip of premaxillaries	325
Width of forehead between bases of horn-cores..	370	417	290
Width at narrowest point between horn-cores and eye-sockets	352	309	256
Width between outer sides of M ₃ at base of crown	157
Width between anterior inner corners of P ₂	106	112
Anteroposterior diameter of orbits.....	70 ^{ap}	72
Length of nasal bones.....	227
Width of nasal bones.....	115	115
Width of nasal bones with curvature.....	133 ^{ap}	135
Distance between tips of horn-cores.....	1000 ^{ap}	826	660
Length of horn-cores along upper curvature.....	385 ^{ap}	275	235
Circumference of horn-cores at base.....	330 ^{ap}	310	212
Dorso-ventral diameter of horn-cores.....	94	102	68
Anteroposterior diameter of horn-cores.....	114 ^{ap}	104	67

* After Chandler 1916A.

^{ap} Approximate measurement.

the fossil and Recent material. Although it seems probable that the material from the asphalt is specifically identical with the Tulare elk, it seems unwise to attempt specific identification on such fragmentary evidence.

Odocoileus sp.

Remains of this form consist mainly of astragali and fragmentary metapodials. These correspond very closely in size to comparable elements in *Odocoileus hemionus californicus*, the Recent California mule deer. Suf-

ficient material is not available, however, to permit positive identification of this form.

ANTILOCAPRIDÆ

Both *Capromeryx* and *Antilocapra* occur in the McKittrick Pleistocene. As shown in figure 6, however, the latter genus is much better represented than the former. At Rancho La Brea *Capromeryx* is clearly the dominant type of antilocaprid.

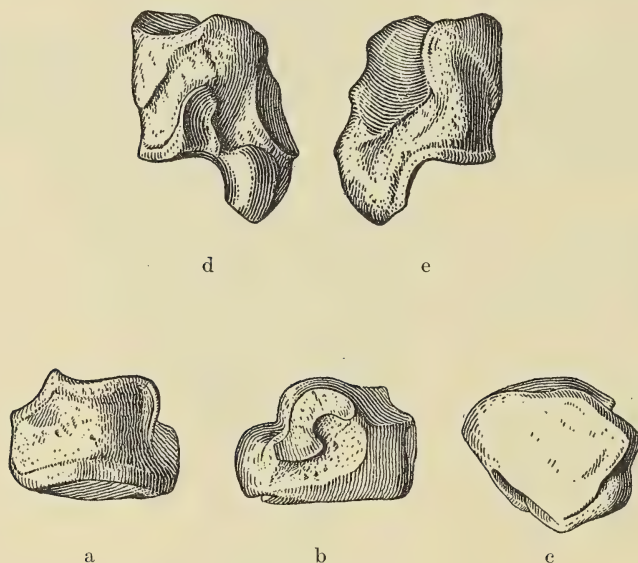


FIG. 10—*Cervus* sp. a-c, right cuneiform, lateral, medial, and superior views; d, e, left unciform, medial and lateral views. Approx. $\times 2/3$.

Capromeryx minor Taylor

The material in the collections of the California Institute consists of two lower molars and a calcaneum, No. 15. According to Furlong (1930, pp. 49-53) the specimens are to be referred to a single individual. No apparent differences seem to exist between the McKittrick material and that of *Capromeryx minor* from Rancho La Brea.

Antilocapra americana (Ord)

The collections of the California Institute include the following: an immature right mandibular ramus, No. 2118, Plate 12, figs. 1, 1a; a mature mandibular ramus also from the right side, No. 2119, Plate 12, figs. 2, 2a; a fragment of skull with the right horn-core, No. 2120, and a horn-core, No. 2121.

Specimen No. 2118 contains the milk-teeth and the first two permanent lower molars. As indicated by Chandler (1916, pp. 116, 117), Dm4 is

three-lobed and the vertical ramus does not make so close an approach to a right angle with the horizontal ramus as is the case in *Capromeryx*.

The mature mandibular specimen, No. 2119, agrees in all particulars with that of *Antilocapra americana*. As shown by table 22, both the teeth and ramus are relatively larger than in *Capromeryx*. The diastema is fully equal in length to the combined measurements of the lower cheek-teeth. As noted by Chandler (1916, p. 117), the anterior mental foramen is quite near the end of the symphysis, while in *Capromeryx* this opening is approximately halfway between P3 and the symphysis.

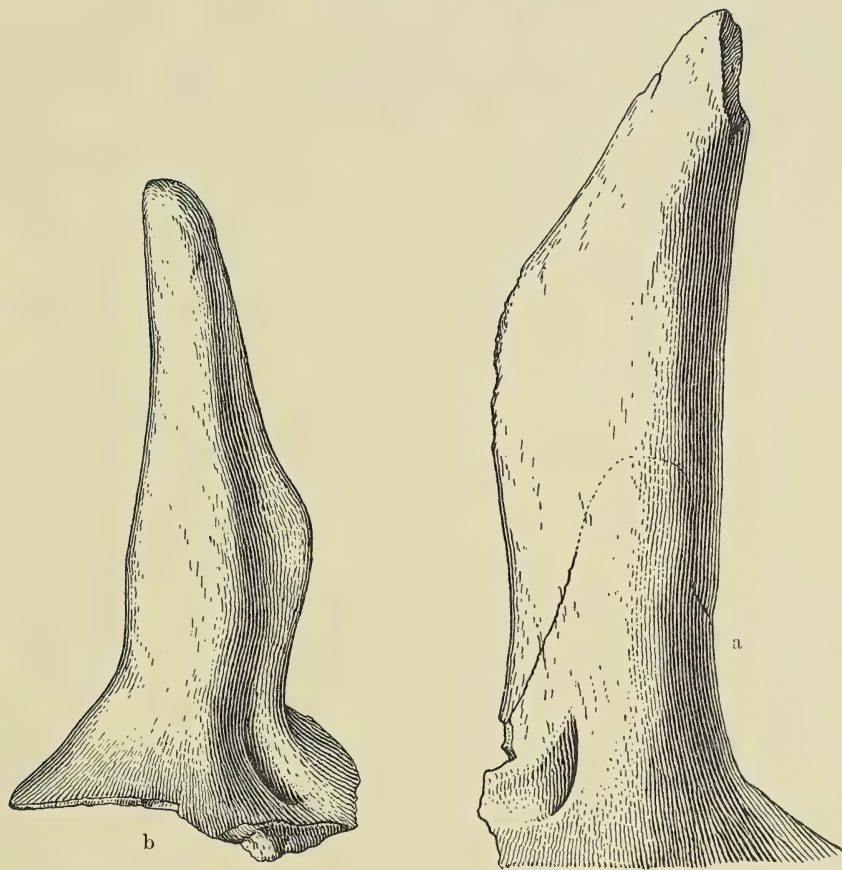


FIG. 11—*Antilocapra americana* (Ord). a, horn-core, C.I.T. No. 2120, inner lateral view; b, horn-core, U.C. No. 33102, inner lateral view. Approx. $\times 2/3$.

The horn-core as noted by Furlong (1931, p. 34) has some resemblances to the corresponding element of *Sphenophalus*. It is relatively broader at the base than a Recent specimen of *Antilocapra*. Compared with the Recent form, the horn is relatively slender and the anterior portion is more distally placed. If as Furlong has indicated, *Antilocapra* is a descendant of *Sphenophalus*, the McKittrick specimens would seem to be somewhat closer to the ancestral type than the average of the Recent forms. However, the asphalt material seems referable to the living species, *A. americana*.

Phalanges II and III, Nos. 2122, 2123, are available. As shown by table 23, all are of relatively large size and exceed corresponding elements of *Capromeryx* in nearly all measurements.

TABLE 21—Measurements (in millimeters) of lower jaw and milk-dentition of *Antilocapra americana*

	Antilocapra 2118	Capromeryx U.C. 12523 *
Length, from posterior margin of anterior mental foramen to angle	131	47 ^{ap}
Depth of ramus below Dm2 measured from the outside.....	16	7.5
Depth of ramus below Dm4 measured from the outside.....	18.2	11
Thickness of mandible across middle of Dm4.....	9.3	5.9
Length of diastema from posterior margin of anterior mental foramen to Dm2.....	37.5	5
Dm2, greatest anteroposterior diameter.....	5.4
Dm2, greatest transverse diameter.....	3
Dm3, greatest anteroposterior diameter.....	7	5.4
Dm3, greatest transverse diameter.....	4.1	3 ^{ap}
Dm4, greatest anteroposterior diameter.....	15	9
Dm4, greatest transverse diameter.....	5.6	3.7

* Type of *C. minor* from Rancho La Brea.

^{ap} Approximate measurement.

TABLE 22—Measurements (in millimeters) of lower jaw and permanent dentition of *Antilocapra americana*

	Antilocapra 2119	Capromeryx U.C. 20036*
Length, from posterior margin of anterior mental foramen to back of M3.....	128
Depth of ramus below P3 measured from the outside.....	25
Depth of ramus below middle of M3 measured from outside.....	29	22
Thickness of ramus below M3.....	13
Length of diastema measured from posterior margin of anterior mental foramen to front of P3.....	56
P3, greatest anteroposterior diameter.....	8.3	4.4
P3, greatest transverse diameter.....	4.7	2.4
P4, greatest anteroposterior diameter.....	8.5	5
P4, greatest transverse diameter.....	5	3
M1, greatest anteroposterior diameter.....	12.5	7
M1, greatest transverse diameter.....	6	4
M2, greatest anteroposterior diameter.....	14	9
M2, greatest transverse diameter.....	7	2.8
M3, greatest anteroposterior diameter.....	24	15 ^{ap}
M3, greatest transverse diameter.....	7

* Rancho La Brea collection.

^{ap} Approximate measurement.

The material in the University of California comprises numerous teeth and two horn-cores, U.C. No. 33102. The shape of these elements corresponds much more closely to that of Recent *Antilocapra americana* than does that of C.I.T. No. 2120.

TAYASSUIDÆ

In view of the rare occurrence of members of this family in the Pleistocene of California, it is not surprising that at McKittrick only a few fragments of peccary have been found. Peccary material from Rancho La Brea is likewise fragmentary and does not permit definite determination, but may represent a species different from the McKittrick form.

Platygonus near compressus Le Conte

Remains of this form consist of a lower jaw fragment, No. 1 C.I.T.; and metacarpal III of the left manus, No. 2 C.I.T. This material was described by Stock (1928, pp. 23-27) and judged to be near *Platygonus compressus*. The metacarpal was compared with a similar element, No. 26004 L.A. Mus. Coll. from Rancho La Brea, and was found to be much larger than the latter. When viewed from the outer side, the shaft of the McKittrick specimen is relatively narrower than in No. 26004 from Rancho La Brea. Measurements and illustrations of the McKittrick peccary are to be found in Stock's paper cited above.

TABLE 23—Measurements (in millimeters) of horn-core and phalanges of *Antilocapra americana*

Horn-core	2120	
Greatest length.....	115 ^{ap}
Greatest anteroposterior diameter.....	45 ^{ap}
Greatest transverse diameter.....	20
Phalanx II	2121	
Greatest length.....	41
Greatest width of distal articulating surface.....	19.5
Greatest anteroposterior diameter of proximal articulating surface	18.5
Greatest transverse diameter of proximal articulating surface	22.5
Phalanx III	2123	U.C. 12521 *
Greatest length.....	24 ^{ap}	17
Greatest dorso-ventral diameter.....	19.5	11
Greatest transverse diameter.....	14

* Rancho La Brea collection.
^{ap} Approximate measurement.

EQUIDÆ

Merriam's study of the horses of Rancho La Brea (1913A) gives a full account of *Equus occidentalis*, the only species of the family found at that locality. The McKittrick horses are discussed in some detail in order to bring out some interesting relationships.

Equus occidentalis Leidy

Horse material from McKittrick is very abundant, and includes almost all parts of the skeleton. Isolated teeth are especially numerous. Char-

acters of skull and mandible are compared with those of the Rancho La Brea material and, except for differences noted in the detailed description, the horses from the two tar deposits appear to be specifically identical.

Skull and Mandible.—In only one instance, C.I.T. No. 1855, Plate 14, figs. 1, 1a, were skull and mandible found in association. This specimen represents a young adult, for all of the teeth are well worn excepting the last upper molar. The skull has been somewhat distorted but is practically complete, for it lacks only the first upper incisors and the paroccipital process on the left side.



FIG. 12—Outlines of skulls of typical horse, Amer. Mus. spec. 16613 (heavy line); *Plesippus shoshonensis* Gidley, C.I.T. No. 1863 (light line); *Equus occidentalis* Leidy, C.I.T. No. 1856 (dotted line); and domestic ass, Amer. Mus. spec. 15675 (dashed line), showing differences in profiles. Figures of Amer. Mus. specimens after Osborn (1912). All figures approx. $\times 1/6$.

The large size and peculiar profile of the skull is very conspicuous. Posterior to the frontals, which are arched both longitudinally and transversely, the occiput slopes upward and backward and terminates in an overhanging crest. Anteriorly the nasals project nearly straight forward except for a slight concavity near their midpoint until they end with a gentle downward slope. This type of profile also characterizes the majority of the Rancho La Brea horses. As in the former, the skull is wide in relation to its length. It would appear, moreover, that arching of the frontals, although marked in the McKittrick specimen, is not so conspicuous as is usually the case in the Rancho La Brea forms. Since the former is slightly distorted, it is difficult to decide to what extent this apparent discrepancy is due to individual variation.

In contrast to the material described from Rancho La Brea the notch between the nasals and premaxillaries is acute for the angle is approximately the same as in the living species. The nasal bones are relatively wide and extend forward to a point within two centimeters of the superior canines. It is inferred that the muzzle was likewise relatively wide.

The occiput is high and narrow. As in the Rancho La Brea species, but unlike the modern horse, the occipital condyles are narrow transversely. As in the former, the maxillary ridges do not extend forward beyond the posterior border of the infraorbital foramen. The latter is located above the middle of P4, a position somewhat farther back than is commonly seen in Rancho La Brea specimens in which this opening is situated above P3.

Just below the naso-maxillary suture and a little above and to the rear of the infraorbital foramen is a long and very shallow groove or lachrymal fossa. This feature is here scarcely so well developed as in *Equus caballus*. The position of the anterior palatine foramen is similar to that in Rancho La Brea specimens and is much the same as in the modern horse. The posterior foramen is situated near the anterior half of M2, a position some-

what farther forward than is usual in the Rancho La Brea material in which this opening is situated opposite the posterior half of M₂. The palatine notch of the posterior nares is in line with the middle of the second upper molars, and is quite narrow. As noted by Merriam, the orbits are relatively large.

It is unfortunate that the sutures are obscure, but the naso-frontal contact and boundaries of the lachrymal bone can be readily distinguished. The forward projection of the former along the middle of the nasals is a broadly open U in shape. This is in sharp contrast to the outline seen in *Equus caballus* where the extension forms a rather well marked V. As in the modern form, the lachrymal bone is roughly quadrangular in outline.

Mandible.—This element is heavy, and in C.I.T. No. 1855 the horizontal ramus is very deep below the anterior cheek-teeth and the first lower molar. This relatively young individual from McKittrick surpasses even old specimens from Rancho La Brea in latter measurement. The great depth of mandible below M₁ is to be accounted for by presence of a distinct convexity of the inferior border of the ramus. The mental foramen is approximately opposite the posterior end of the symphysis. In this feature and in the relatively great width of the symphysis the McKittrick and Rancho La Brea horses are much alike.

Additional Skull Material.—Skull No. 1856 C.I.T., Plate 13, is of an individual slightly older than No. 1855. In No. 1856 all the teeth are well worn, but the inner enamel ring of I₁ is still present. The specimen lacks both bullæ and paroccipital processes as well as the left zygomatic arch. The frontal region has been somewhat crushed, but not sufficiently to obliterate any important characters.

In profile this skull resembles No. 1855 rather closely. The nasals, however, show no trace of concavity and the overhang of the occipital crest is a trifle less pronounced. In these respects No. 1856 resembles the typical Rancho La Brea horse more closely than does No. 1855. In contrast to the latter, No. 1856 is much longer and relatively narrow. Reference to table 25 shows that while the two differ in length by 40 millimeters, the greater part of the difference is confined to the facial region, for there is a difference of 33 millimeters in the distance from the anterior end of the premaxillaries to a line connecting the posterior borders of the orbits. Reference to Merriam's paper shows that No. 1855 corresponds in its measurements to a young adult from Rancho La Brea, while No. 1856 surpasses all specimens in distance from the anterior borders of the orbits to the anterior margin of the premaxillaries. This would appear to be merely an individual variation for in all other characters No. 1856 closely resembles the more usual type of skull from Rancho La Brea. It should be noted, however, that the longer-faced form exhibits a more nearly V-shaped projection of the naso-frontal suture than No. 1855.

Specimen No. 1859 C.I.T. is of a young individual. The first upper molar on the right side is in use, but the corresponding tooth on the left side is just emerging, as are the canines and last upper molars. This specimen is quite incomplete, for the posterior portion of the skull is broken off at the orbits.

The most interesting feature of this skull is that it shows to a greater degree than any other from McKittrick the arching of the frontal region which is so characteristic of the species. The naso-frontal suture ends anteriorly in a rather well marked V-shaped projection. As in young individuals from Rancho La Brea, the posterior palatine foramen is located

near the anterior half of M₂. The anterior margin of the posterior nares is situated opposite the middle of M₁.

Two incomplete skulls of very young individuals are available: one, No. 1860 C.I.T., possesses milk-teeth in an early stage of wear with M₁ just emerging from the left side of the palate; the other, No. 1858 C.I.T., represents a somewhat younger stage, for the milk-teeth are scarcely worn. The former has had to be restored in the occipital region, and lacks most of the rostrum; while the latter wants both the rostrum and condyles, as well as the left zygomatic arch.

Both skulls show an overhanging occipital crest. In addition, No. 1860 shows the profile characteristic of older individuals. The infraorbital foramen is located above the anterior half of Dm₃; while the anterior borders of the postpalatine foramina and posterior nares are situated on a line connecting the centers of the last upper milk-teeth. The naso-frontal suture is well shown in No. 1858, and possesses a well marked V-shaped projection.

Summary of Skull Characters.—A survey of the material described above indicates that while the various specimens probably belong to the same species there is, nevertheless, considerable individual variation. This is most marked in the degree of arching of the frontals, overhang of occipital crest, and in outline of forward extension of the naso-frontal suture which varies from a broadly open U to a V in shape. Variations in size are shown by table 25. Changes during growth do not appear to be very important and are manifest mainly in a backward shifting of the postpalatine foramen and a lengthening of the facial region with advancing age.

Dentition.—All of the cheek-teeth are very long, moderately curved, and are well cemented. The anterior margins of the first two upper incisors fall into a vertical plane when the skull is laid top down upon a horizontal surface. Both upper and lower incisors are wide, and there is no evidence of a cup in I₃, although an inner enamel fold is always present in the third upper incisor. Compared to *Equus caballus* the canines are of moderate size, and are laterally compressed in young individuals. P₁ is never present in the McKittrick material, but a small P₁ is found in some of the Rancho La Brea specimens. In all other respects the permanent dentition of the McKittrick specimens is so similar to that of the Rancho La Brea horses as described by Merriam that a detailed description is unnecessary.

Upper Deciduous Cheek-Teeth.—C.I.T. No. 1862, Plate 14, fig. 2, shows the enamel pattern in a section which corresponds to an early stage of wear. Both para- and mesostyle are heavily developed. The latter style is almost as broad as the parastyle in all cases excepting Dm₂, where in consequence of the unusually small size of the parastyle it is much the larger of the two. The fossettes are much larger than in the permanent teeth, but show the same principal folds and in addition some tiny plications not seen in the latter. Pre- and postfossettes are united in the second and fourth upper milk-molars, but in deeply worn teeth the lakes are separate and much smaller in size.

The protocone is long, relatively narrow, and shows nearly smooth inner borders in the second and third milk-premolars. It is noteworthy that in both of these teeth the inner pillar does not project forward beyond the isthmus. In Dm₄, however, this cusp is longer and somewhat indented, and in addition the anterior margin projects forward to a degree as great as any seen in the permanent teeth. In all cases the isthmus is very narrow. The post-protoconal valley, on the other hand, is very wide and is marked

by a well defined pli caballin on its anterior margin. The hypocone is distinct and scroll-like in outline.

Lower Deciduous Cheek-Teeth.—The enamel pattern of these teeth does not differ greatly from that of the permanent premolars. The most significant departure, perhaps, is presence in the milk-teeth of an outward folding of the enamel (protostylid) on the antero-external margin of the protoconid. However, this fold is not well developed in all of the lower milk-teeth.

It is perhaps not unduly speculative to remark that the pattern shown by both upper and lower milk-teeth is in many respects that which would have to be postulated, if it is assumed that *Equus* has been derived from *Pliohippus*, through the intermediate genus, *Plesippus*.

Individual Variation.—As noted by Merriam, the protocone of the permanent upper dentition varies greatly in size and is also subject to minor variations in shape. The proto- and hypoconid may vary from a concave to a convex shape in individual instances and this is especially true for the molar teeth. In the premolars the outer walls of these cusps are almost always flat or indented. Table 26 shows the differences in size, and it will be noted that in nearly all instances the measurements correspond closely to those of comparable individuals from Rancho La Brea.

Limb and Foot Elements.—There appears to be little difference between *Equus occidentalis* and the Recent horse insofar as the limb and foot elements are concerned. The ungual phalanges are considerably smaller in *E. occidentalis*, however, and this is only one character among many in which the Pleistocene horse compares very closely with *Equus asinus*. In contrast to *Plesippus shoshonensis* (see Plate 15), *Equus occidentalis* is distinguished by somewhat more robust limb proportions and slightly shorter splints. However, these are merely average differences and are not always to be found in individual instances.

Relationships.—Only two relationships need to be discussed: one which prevails between *Equus occidentalis* and *Plesippus*; the other which exists between *E. occidentalis* and the asses.

Relation of Equus occidentalis to Plesippus.—On a former occasion the writer (1936) attempted to show that the Pleistocene genus, *Equus*, has descended from the upper Miocene-Pliocene genus, *Pliohippus*, through intermediate forms which are included in the late Pliocene genus, *Plesippus*. In this connection it is interesting to note that Matthew (1929A) considered *Equus occidentalis* to be intermediate between *Plesippus* and *Equus*. Since the evidence for this conclusion was not stated by Matthew, it seems desirable to compare *Plesippus* and *Equus occidentalis*.

Characters common to *Plesippus* and *Equus occidentalis* are: (1) overhanging occipital crest, (2) heavy mandible with distinct convex inferior border below M₁, (3) presence of protostylid in lower milk-teeth, and (4) relatively small feet and slender limb elements. It should be noted, furthermore, that the relatively simple fossette borders seen in *Equus occidentalis* are more characteristic of *Plesippus* than of *Equus*.

There are, however, some important differences between the two genera. When the skull profile of *Equus occidentalis* is superimposed upon that of *Plesippus shoshonensis* it is readily seen that overhang of the occipital crest is more marked in the latter. In addition, the frontals are somewhat more arched in *Equus occidentalis*. Another and no less striking departure is apparent lack of a pli caballin in the molar teeth of the Pleistocene form. Perhaps most significant of all is the presence of a well marked lachrymal fossa in *Plesippus shoshonensis* and its almost total absence in

the McKittrick species. In short, differences between *Equus occidentalis* and *Plesippus*, although marked, are only those that might be expected if *Plesippus* is intermediate between *Pliohippus* and *Equus*. In this connection the rather primitive characters of the milk-teeth of *Equus occidentalis* should be recalled. In view of the late Pleistocene age of the McKittrick species, it is remarkable that it should retain so many characteristics of the horses of the late Pliocene.

The writer's views as to the ancestry of *Equus* are at variance with those expressed by Stirton (1934, pp. 382-383). This author places *Plesippus* in the rank of a subgenus of *Equus*, and regards *Calippus*, a middle Pliocene form, as the ancestor of the living genus. Evidence for these conclusions rests upon isolated teeth, which are long-crowned, only moderately curved, and show an *Equus*-like enamel pattern. The first is most significant, for on the basis of enamel pattern alone it would appear that *Neohipparion princeps* (Matthew, 1924, p. 166), *Calippus*, and *Plesippus* are all ancestors of *Equus*. When it is recalled that *Equus* has been described from the late Pliocene of Europe, there would appear to be good reason to derive the living genus from middle Pliocene or even earlier ancestors. On the other hand, the late Pliocene form from Europe, *Equus stenonis*, possesses many characters which might lead one to regard it as a species of *Plesippus*. The genus *Equus* would thus be limited to the Pleistocene and Recent.

From the well marked *Equus*-like enamel pattern of *Calippus* it appears necessary to assume that it diverged from the parent stock as far back as perhaps the late Miocene. On this assumption it is difficult to account for the many rather primitive characters shown by *Equus occidentalis*. Abnormalities usually thought to be atavistic in nature are sometimes encountered in living horses (Lydekker, 1912, pp. 59-60), but in the McKittrick form such relatively primitive characters as simple bordered fossettes and unindented protocone in the molar teeth might almost be said to characterize the species. Rounded proto- and hypoconids are, moreover, by no means rare. In other words, as we go back in time the characters of *Equus* converge quite rapidly toward *Pliohippus*, and by the late Pliocene have almost merged with those of the latter. For this reason it appears plausible to regard *Calippus* as a rather precocious offshoot of the *Protohippus* group, but not in the direct line to *Equus*. In other words, *Calippus* appears to be too advanced at too early a date to be the ancestor of *Equus*, for the earliest species of the latter genus are more primitive in tooth structure than *Calippus*, the supposed middle Pliocene ancestor.

Relation of Equus occidentalis to the Asses.—The many characters which distinguish the living forms, *Equus caballus* and *Equus asinus*, have been evaluated and compiled by Osborn (1912, pp. 88-92), and table 24 is based on the work of that author.

In addition to the distinctions tabulated above, two others have been cited by Lydekker (pp. 42-44). According to that author *Equus asinus* is characterized by smaller and narrower ungual phalanges, with a deeper and broader frog than is seen in the horse. Lydekker comments that the type of frog found in *E. asinus* is probably an adaptation fitting the animal to a more rocky terrain than is frequented by horses. However that may be, it will be noted that the ungual phalanges of *Equus occidentalis* are relatively small and narrow with a broad and deep cavity in their lower surface.

Referring to table 24, it is seen that out of the eleven distinctions listed, *Equus occidentalis* approximates *Equus asinus* in the first eight. In the remaining three the McKittrick form resembles the horses, but it should

be noted that shape of the naso-frontal suture in *Equus occidentalis* is subject to considerable individual variation, and is in some respects intermediate between that of the horses and asses. That certain North American Pleistocene horses resemble *Equus asinus* has been known for a long time and it would appear that despite its relatively large size *Equus occidentalis* is to be included in this group. It is interesting to recall that Boule (1910, p. 132) noted the presence of asses in the European Pleistocene and remarks that by this time the horses were already highly diversified.

TABLE 24—Major distinctions between *Equus caballus* and *Equus asinus*

	<i>Equus caballus</i>	<i>Equus asinus</i>
Orbit.....	Longitudinal diameter greater than vertical	Both diameters nearly alike, vertical may be greater than horizontal
Mandible.....	Inferior border of horizontal ramus smooth and straight, seldom convex	Inferior border furnished with prominences, thicker than in horse, convex
Forehead.....	Nearly straight	Convex
Occipital crest.....	Continues curve of occiput	Prominent
Line drawn from anterior end of maxillary ridge to a point just above external auditory meatus (Line of Lesbre)...	Passes below occipital crest	Passes through occipital crest
Height of skull at occiput, mandible included....	Relatively low	Relatively high
Occiput vertex angle....	More nearly perpendicular	More nearly retrocumbent
Enamel pattern of upper cheek-teeth.....	Pli caballin distinct	Pli caballin lacking in molars
Nasal-frontal suture.....	V-shaped	A nearly straight line
Nasal-lachrymal suture...	Nearly a straight line parallel to long axis of skull	Concave (not characteristic of Asiatic asses)
Postorbital process.....	Three-sided	Oval and compressed

As has been noted in the section concerning the relation of *Equus occidentalis* to *Plesippus*, certain characters of the asses are also to be seen in the late Pliocene genus. It would appear, therefore, that *Plesippus* represents the parent stock from which descended the three major divisions of the modern horses. According to this postulate, the ass and zebra have undergone less modification than the horse, and the cleavage giving rise to various lines began sometime in the late Pliocene or early Pleistocene.

NOTE ON A LARGE VARIANT OF *EQUUS OCCIDENTALIS* AND THE STATUS OF *EQUUS PACIFICUS*

In the collections of the University of California are several isolated permanent and deciduous upper cheek-teeth, noteworthy because of their large size. No less than four individuals are represented in this collection, and from them a composite right cheek-tooth series has been assembled. In addition to their large size (see table 27), these teeth are remarkable in that the enamel pattern of the fossettes is somewhat more complicated than

TABLE 25—Measurements (in millimeters) of skull and mandible of *Equus occidentalis*

Skull	1856 ^a	1861 ^b	1859 ^c	1857 ^d	1855 ^e
Length from anterior end of premaxillaries to posterior end of condyles.....	575	580	535 ^{ap}
Length from anterior end of premaxillaries to inferior margin of foramen magnum	546	556	507 ^{ap}
Length from anterior end of premaxillaries to a line connecting anterior border of second upper premolars.....	151	148	153	134 ^{ap}
Length from anterior end of premaxillaries to a line connecting posterior border of last upper molars.....	335	340	330 ^{ap}	327 ^{ap}
Length from anterior end of premaxillaries to a line connecting anterior borders of orbits.....	369	336 ^{ap}	334	325 ^{ap}
Length from anterior end of premaxillaries to a line connecting posterior borders of orbits.....	426	393 ^{ap}
Least width across rostrum.....	68	68
Width of skull on maxillary ridge at maxillo-malar suture	190	183	201	180
Greatest width across posterior border of orbits	224
Width between outer sides of second upper premolars.....	108	107	109	116	105 ^{ap}
Width between outer sides of last upper molars	134 ^{ap}	122 ^{ap}	116	132	114 ^{ap}
Greatest anteroposterior diameter of orbits	60	71	65
Height of occiput above base of occipital condyles	115	127 ^{ap}
Least width of occiput below superior crest	66	62 ^{ap}
Mandible					
Greatest anteroposterior diameter measured along one ramus.....	427
Anteroposterior diameter of symphysis...	80 ^{ap}
Least width of symphyseal region.....	46
Height below anterior end of P ₂ measured normal to inferior border.....	65
Height below anterior end of M ₁ measured normal to upper border.....	100

^a Young adult, M₃ in function; inner enamel ring of I₁ still present.^b Individual of about the same age as above.^c Young individual, M₃ just emerging.^d Old individual, all teeth well worn.^e Young adult, M₃ just coming into use.

All specimens in the collections of the California Institute of Technology.

^{ap} Approximate measurement.

is usually the case in *Equus occidentalis*. Two cheek-tooth series from Rancho La Brea, L.A.M. Nos. 3500-22 and 3500-R-5, agree very closely in size and outline of enamel pattern with the teeth in question. As is shown by table 27, although the anteroposterior diameters of the McKittrick specimens usually exceed those from Rancho La Brea, the transverse

measurements of teeth from the two localities are approximately the same. Comparison of tables 26 and 27 indicates that in latter dimension the teeth in question exceed the average of *Equus occidentalis* by more than three

TABLE 26—Measurements (in millimeters) of permanent dentition of *Equus occidentalis* *

Upper Dentition	1857 ^a	1856 ^b	1861 ^c	1855 ^d	1859 ^e
Length of upper molar-premolar series...	192	180	184	190	192
Length of upper premolar series without P1	102	100	100	102	104
Length of upper molar series.....	89	80	83	87	88
P2, anteroposterior diameter	39	37.3	40	39	39.6
P2, transverse diameter	27.5	27	28	27.8	26.5
P2, length of protocone	8.5	9.7	11.9	11.4	10.8
P3, anteroposterior diameter	31.7	32.6	29.6	32	33
P3, transverse diameter	31.2	30	30	29.6	28
P3, length of protocone	13	13.8	14	14	14
P4, anteroposterior diameter	30	30	29.5	32	29.7
P4, transverse diameter	30.2	27.8	28.5	28	26
P4, length of protocone	13.1	14.5	17.2	15	10.5
M1, anteroposterior diameter	28.1	25.2	26	27	29
M1, transverse diameter	30.7	28.2	27.8	27	29
M1, length of protocone.....	12.8	13	14	14.8	15
M2, anteroposterior diameter	27.8	27.5	27.2	29	30
M2, transverse diameter	27	27.8	26	27	27
M2, length of protocone.....	12.8	15	15.8	15	15
M3, anteroposterior diameter	30	26.8	26	27
M3, transverse diameter	23.2	20.2	19.6	22
M3, length of protocone	14	14	13	15
Lower Dentition					
Length of lower molar series.....	83
Length of lower premolar series.....	99
P2, anteroposterior diameter	34.2
P2, transverse diameter	16.2
P3, anteroposterior diameter	31
P3, transverse diameter	17.8
P4, anteroposterior diameter	33
P4, transverse diameter	15.8
M1, anteroposterior diameter	28.2
M1, transverse diameter	16.2
M2, anteroposterior diameter	28.5
M2, transverse diameter	15.5
M3, anteroposterior diameter	25
M3, transverse diameter	11.2

* For system of measurements see Merriam (1913, p. 409).

^a Old individual, all teeth well worn.

^b Young adult, M3 in function; inner enamel ring of I1 still present.

^c Individual approximately of the same age as ^b.

^d Young adult, M3 just coming into use.

^e Young individual, M3 just emerging.

All specimens in the collections of the California Institute of Technology.

millimeters. As has been pointed out by Gidley (1901, pp. 105-106) this measurement seems to be quite constant in living horses of the same species, and according to the views of that author (*op. cit.*, pp. 102-103) the large

teeth in both the McKittrick and Rancho La Brea collections should be referred to distinct species. However, in the writer's opinion there is less justification for this view than for the assumption that they merely represent large end members of the *Equus occidentalis* group.

A cast of the type of *Equus pacificus*, a P3, in the collections of the California Institute measures 34 mm. in anteroposterior diameter and 32 mm. in transverse. As will be seen from table 27, this tooth exactly corresponds in size to large specimens of *Equus occidentalis*. While *Equus pacificus* is usually thought of as possessing a somewhat more complicated enamel pattern, it must be noted that the type does not substantiate this view.

TABLE 27—Measurements (in millimeters) of large variant of *Equus occidentalis*

Permanent Dentition	McKittrick		Rancho La Brea	
	U.C. 33101	U.C. 33101	L.A.M. 3500-22	L.A.M. 3500-R-5
P2, anteroposterior diameter.....	41	40
P2, transverse diameter.....	30	30
P3, anteroposterior diameter.....	34	34	29	32
P3, transverse diameter.....	33.4	33	32.5	29.8
P4, anteroposterior diameter.....	32.5	31.2	31
P4, transverse diameter.....	32.8	32.8	31.8
M1, anteroposterior diameter.....	34.5	26.5	29
M1, transverse diameter.....	29.8	29	28.3
M2, anteroposterior diameter.....	36.4	28	28
M2, transverse diameter.....	31	30.5	27
M3, anteroposterior diameter.....	32	31.5	28
M3, transverse diameter.....	26	27	20.5
Milk-Dentition			3500-27	3500-32
Dp2, anteroposterior diameter.....	47	47.4
Dp2, transverse diameter.....	26	26
Dp3, anteroposterior diameter.....	35.5	32.5	32.5
Dp3, transverse diameter.....	28.5	26	27
Dp4, anteroposterior diameter.....	38.6	36	36
Dp4, transverse diameter.....	29.5	26	25.5

Therefore, it seems advisable to consider *Equus pacificus* as a synonym of *Equus occidentalis*. As a matter of fact this was actually done by Leidy (1873, p. 332) but at a later time Gidley (1901, pp. 116-118) re-instated *E. pacificus*, largely upon characters of referred material from Fossil Lake. The large teeth with complicated enamel pattern from this locality referred by Gidley to *Equus pacificus* possess few characters other than size to substantiate the reference. Since the large teeth from the asphalt deposits equal the latter in size, but in enamel pattern are very similar to *E. occidentalis*, it seems best from the writer's point of view to regard *E. pacificus* as invalid, and to regard the status of the Fossil Lake materials as an open question. The latter may also be referred to *E. occidentalis*, but are more probably a new or some previously described species other than *Equus occidentalis* (*E. pacificus*).

ELEPHANTIDÆ

Representatives of this family are rare at McKittrick and consist of only fragmentary remains which apparently are to be referred to *Parelephas columbi*. There is no evidence that the species *Archidiskodon imperator* existed in the McKittrick area during the period of fossil accumulation. Whether absence of this form should be attributed to chances of preservation and collecting or to environmental factors, remains an open question.

Parelephas columbi (Falconer)

This species is represented by a single last upper molar, No. 2125 C.I.T., Plate 16. There are on the average seven enamel plates in a 100-millimeter line. Thus the number of plates within this distance appears to be too great for *Archidiskodon imperator* and is of the right order of magnitude for *Parelephas columbi*. The maximum length of this tooth is approximately 240 mm.; its greatest width 78 mm.

MASTODONTIDÆ

Only one species, *Mastodon raki* is recorded from the McKittrick tar seeps.

Mastodon raki Frick

This species seems to be represented in the collections of the University of California by a fragment of upper tusk, No. 35118; a right mandibular ramus containing M1 and M2, No. 33117, Plate 17, figs. 3, 3a; a fragment of left mandibular ramus containing M1 and M2, No. 33116; a left M3, No. 33115, Plate 17, fig. 2; a deeply worn M1, No. 33119; a fragment of mandibular ramus containing Dm2, Dm3, and Dm4, No. 22120, Plate 17, fig. 1; and a few isolated foot elements in addition to an almost complete foot.

The upper tusk is too fragmentary to furnish much information other than that the tooth was large and possessed a gentle upward curvature.

Ramus No. 33117 is broken at the symphyseal end, and it is impossible to discover whether lower tusks were present or not. The symphyseal trough is likewise imperfectly preserved, but this feature seems to have been much the same as in *M. americanus* and *M. raki*.

M1 shows a well developed cingulum around the entire tooth, except for the internal border, where the enamel is too broken to leave any reliable indications. This tooth has three crests, and there are indications of trefoils on the outer cusps.

M2 also has three crests and shows the presence of a well developed cingulum on all sides except the internal one. The posterior cingulum is especially well developed. The outer cusps show trefoils on both their posterior and anterior margins. Each of the principal cusps carries a median conelet. The conelets of the inner cusps, however, are larger than those on the outer ones. The valley between the crests is acute. The crests are very high (see table 28).

M3 possesses four fully developed transverse crests, with the fifth partially formed, and a small heel. This tooth shows the presence of only the anterior cingulum. The outer cusps show trefoils on both their anterior and posterior margins. As in M2, the second and third crests show median conelets on both the inner and outer cusps. The valley between the crests is acute, and is shaped much as in *Mastodon acutidens* (Osborn, 1936, pp. 696-697). However, the McKittrick specimen does not possess the

knife-like grinding surface of Osborn's species. There appears to be a deposit of cement in the valleys, which is especially thick in the first two anterior depressions. This tooth is relatively long and narrow (see table 28), for the index is only 43 as compared with 54 for the American mastodon (Osborn, 1936, pp. 175-176). In characters of M $\bar{3}$ the McKittrick specimen agrees very well with *Mastodon raki* (Frick, 1933, p. 630). Since the index of this tooth and presence of cement in the valleys are the two principal characters of *Mastodon raki*, it seems necessary to refer the McKittrick material to Frick's species.

M $\bar{1}$ is too deeply worn to show much more than that the tooth was three-crested and possessed the same shape as the corresponding tooth of *M. americanus*.

TABLE 28—Measurements (in millimeters) of dentition of *Mastodon raki*

	U.C. 33120
Dm $\bar{2}$, anteroposterior diameter.....	29.4
Dm $\bar{2}$, transverse diameter.....	23
Dm $\bar{3}$, anteroposterior diameter.....	48.7
Dm $\bar{3}$, transverse diameter.....	36
Dm $\bar{4}$, anteroposterior diameter.....	60 ^{ap}
	U.C. 33116
M $\bar{1}$, anteroposterior diameter.....	93.2
M $\bar{1}$, transverse diameter.....	70
M $\bar{2}$, anteroposterior diameter.....	117
M $\bar{2}$, transverse diameter.....	76
M $\bar{2}$, height of middle crest.....	44.2
	U.C. 33115
M $\bar{3}$, anteroposterior diameter.....	163
M $\bar{3}$, transverse diameter at third crest.....	74.2
M $\bar{3}$, height of second crest (exclusive of cement).....	47.5

ap Approximate measurement.

The ridge formula of the deciduous teeth agrees with that of the American mastodon as determined by Osborn (1936, p. 152). Dm $\bar{2}$ is small with two ridge crests and is bilophodont. Dm $\bar{3}$ is larger than Dm $\bar{2}$, is bilophodont, and each lobe carries two crests. In addition, this tooth possesses a large talon. Dm $\bar{4}$ is not well preserved, but as in *M. americanus* this tooth is larger than Dm $\bar{3}$, and is trilophodont.

In summary, it can be said that although the McKittrick mastodon in some respects agrees closely with *M. acutidens* and *M. americanus*, there does not seem to be sufficient reason for referring the material to any species other than *M. raki*. Since Frick's species was obtained from deposits at Hot Springs, New Mexico, which are presumably of late Pleistocene age, very little chronological significance is to be attached to the specific reference of the McKittrick mastodon.

RODENTIA

As mentioned on page 151, representatives of this order are relatively more abundant at McKittrick than at Rancho La Brea. Furthermore, the latter assemblage is recorded to include extinct species, but the McKittrick collection seems to consist entirely of living forms. The difference may indicate that the McKittrick rodent fauna is largely post-Pleistocene in age, and this conclusion seems to be substantiated by the inference that the rodent assemblage indicates arid conditions. As noted on page 132, however, material in all conditions of preservation is included in the rodent assemblage, and it seems very improbable that all specimens of this order are of Recent age.

While, as mentioned on pages 155-156, a slight time difference may exist between McKittrick and Rancho La Brea, the discrepancies in the rodent faunas are too great to be attributed entirely to this cause. A revision of the Rancho La Brea rodents is beyond the scope of this work, but it is the writer's opinion that many of the extinct types listed from the Los Angeles locality are founded on inadequate material.

SCIURIDÆ

McKittrick is somewhat richer than Rancho La Brea in representatives of this family, for in addition to *Otospermophilus grammurus* which is common to both localities, the San Joaquin Valley occurrence includes a species of antelope ground squirrel, *Ammospermophilus* cf. *nelsoni*, not yet recorded from the Los Angeles locality. However, none of the Sciuridæ is particularly abundant at McKittrick.

Otospermophilus cf. *grammurus* (Say)

A right and a left mandibular ramus in the collections of the California Institute of Technology are referred to this species. The former lacks all teeth excepting the first two lower molars; the latter contains only the lower premolar, which by its sub-triangular form serves to mark the genus, *Otospermophilus*. The size and tooth pattern of both specimens is very close to that of *Otospermophilus grammurus grammurus*, but the fragmentary nature of the remains permits a comparison rather than an identification with that form.

Ammospermophilus cf. *nelsoni* (C. H. Merriam)

No satisfactory criteria for differentiating *Ammospermophilus* from *Callospermophilus* are to be found in the literature. An examination of skulls and mandibles of living forms indicates that *Callospermophilus* possesses a larger P₃ and somewhat higher cusped teeth than does *Ammospermophilus*; while in the lower jaw P₄ of the latter is more nearly triangular in outline, and the trigonids of all teeth appear to be lower. In addition the angle appears to be somewhat more nearly horizontal in *Callospermophilus* than in *Ammospermophilus*. It must be admitted that the above criteria were not tested by examination of all known species of the two genera, but they appear to hold insofar as forms which still live in or near the McKittrick area are concerned. It is interesting to note that if these criteria are correct, *Callospermophilus* is closer to the ground squirrel, *Citellus*, than is *Ammospermophilus*. The latter resembles the tree squirrel, *Sciurus*, much more closely than its habits might lead one to suspect. The

material in the collections of the California Institute of Technology, which consists of nine right and nine left mandibular rami, is evidently to be referred to *Ammospermophilus*, and insofar as size and tooth pattern are concerned appears to be quite close to the species *A. nelsoni* which still lives in the McKittrick area. A fragmentary left maxillary containing P₄ and the first two upper molars is also referred to this species.

GEOMYIDÆ

As at Rancho La Brea only one species of gopher is recognized at McKittrick.

Thomomys bottæ bottæ (Eydoux and Gervais)

The material in the California Institute collections consists of two fairly complete and eight fragmentary skulls in addition to 31 more or less complete mandibles, which represent not less than 16 individuals. Although there is considerable size variation in this series it is usually possible to correlate this with stage of growth, and there thus appears to be little reason for considering more than one species to be represented in the collection.

HETEROMYIDÆ

Only two species of this family occur at McKittrick: *Dipodomys* near *ingens* and *Perognathus* cf. *inornatus*. The great abundance of representatives of *Dipodomys* points to environmental conditions similar to those prevailing in the area today, but there seems to be some reason for considering most of the heteromyids from the tar seeps as Recent in age.

Dipodomys near *ingens* (C. H. Merriam)

The collections of the California Institute of Technology contain no less than 255 individuals of this species, for they include this number of left mandibular rami, an almost equal number of the corresponding element from the right side, and 51 more or less complete skulls.

According to Wood (1935, pp. 148-155) *Dipodomys* is distinguished from *Microdipodops* by a less pronounced inflation of the bullæ than in the latter. In *Dipodomys* the bullæ do not extend below the level of the cheek-teeth, while in *Microdipodops* they extend somewhat below this level. The single rather perfect skull, although considerably smaller than in most individuals of the *Dipodomys ingens* group, agrees in these characters with the genus *Dipodomys*. No other characters can be found which separate the McKittrick material from this genus, for the variation in size can usually be correlated with stage of individual growth. In all characters the average of the specimens is close to *Dipodomys ingens*, but since few specific characters are exhibited by the material it is not possible to identify positively the McKittrick kangaroo rat with the above species.

Since variation in size is quite marked in the McKittrick specimens, it is impossible to give in a limited space a table which would adequately express the average proportions. In all measurements, however, the material averages close to those of *Dipodomys ingens*.

Perognathus cf. *inornatus* C. H. Merriam

This genus has been identified by the wing-like outward inflection of the descending process of the ramus. The material in the collections of the California Institute of Technology consists of nine rather imperfect mandi-

bular rami, none of which possesses the full complement of teeth. Few, if any, specific characters are shown by this material, but all the specimens are close in size to *Perognathus inornatus*, a form which still inhabits the McKittrick area.

CRICETIDÆ

Separation of genera of this group is difficult. Much of the McKittrick cricetid material has lost all diagnostic characters and must remain indeterminate. It seems reasonably certain, however, that all five of the Rancho La Brea cricetine genera—*Onychomys*, *Reithrodontomys*, *Peromyscus*, *Neotoma*, and *Microtus*—are present in the McKittrick collection.

Onychomys? sp.

According to Wilson (1933, p. 71) this genus is distinguished from *Peromyscus* by the following characters: in the mandible the coronoid process is better developed in *Onychomys*, while in the grasshopper mouse the ascending ramus makes a somewhat greater angle with the alveolar portion of the jaw than in *Peromyscus*.

Following the same author, *Onychomys* is distinguished from *Reithrodontomys* by the character of descending process of the ramus. In *Reithrodontomys* this portion of the ramus is bent into a more nearly horizontal position than in *Onychomys*, and the extreme edge is twisted upward, leaving a depression. Furthermore, in *Onychomys* the coronoid process is less strongly developed than in the grasshopper mouse.

It would appear, therefore, that the only *Onychomys*-like specimen in the collections of the California Institute of Technology, which has the descending ramus completely preserved is to be referred to the grasshopper mouse. This specimen is approximately of same size as a mandibular ramus from Carpinteria tentatively referred to the grasshopper mouse. As noted by Wilson (1933, p. 72), the Carpinteria material is of relatively large size, but is within the range of variation of *Onychomys torridus* and *O. torridus ramona*. Some of the mandibular rami which lack the descending ramus, and are tentatively referred to *Peromyscus*, may actually represent the genus *Onychomys*.

Reithrodontomys? sp.

Characters separating this genus from *Onychomys* have been listed in the preceding section. With regard to the mandible Wilson (1933, p. 73) quotes from Howell:

"Descending process of mandible a broad flattened plate, strongly inflected inward, the lower portion twisted into a nearly horizontal position and the inner margin raised, leaving a distinct depression in the ramus . . ."

Wilson also states that the upper incisors of *Reithrodontomys* are grooved.

There are in the collections of the California Institute four imperfect mandibular rami, one of which contains P₄. All lack the descending process of the ramus, but by their very small size they seem referable to the harvest mouse. While the specimens may be merely immature forms of *Peromyscus*, the presence of numerous, very small grooved upper incisors in the collection of detached teeth seems to verify the presence of *Reithrodontomys* in the McKittrick rodent collection. Some of the small specimens tentatively referred to *Peromyscus* may actually belong to this group.

Peromyscus cf. californicus (Gambel)

The material in the California Institute collections consists of approximately 100 left mandibular rami and nearly 90 corresponding elements of the right side. Apparently all stages of growth are represented by these individuals. As has been noted in preceding sections, however, it is possible that some of the smaller specimens are to be referred to either *Reithrodontomys* or *Onychomys*. In size and in characters of the teeth, the average of this material is quite close to *Peromyscus californicus californicus*, but since few specific and subspecific characters are present, it is impossible to state definitely whether or not the two additional varieties of deer mice, *P. maniculatus gambelii* and *P. boyleyi rowleyi*, which also inhabit the McKittrick area, are present in the fossil assemblage. It seems probable that they do occur in the collection.

Neotoma lepida gilva Rhoades

The wood rat is represented in the collections of the California Institute by two right and one left mandibular rami. This material has been identified by Emmet Hooper of the Museum of Vertebrate Zoology, University of California, who finds no difference between the asphalt material and the form still inhabiting the McKittrick area.

Microtus californicus cf. æstuarinus R. Kellogg

According to Kellogg (pp. 15-18) this variety is distinguished by its large size; long, angular skull with ridges strongly converging in the interorbital region, but always with a definite sulcus between them. The dorsal profile of the skull is convex with the exception of the interorbital region, where it is somewhat depressed. The upper teeth preserve the typical *M. californicus* pattern, but the anterior loop of M₁ is crescentic. An internal lobe is usually present on the posterior triangle of M₂. The long terminal loop of M₃ is variable in outline, and is usually crescentic, but sometimes is strongly indented by a notch. Internally the loop is notched by a deep re-entrant angle.

The mandible is robust and heavier than in *M. californicus*. The lower molars are similar in pattern to those in other members of the genus, excepting that the posterior transverse loops are proportionally wider.

The material referred to this subspecies in the collections of the California Institute consists of 35 left mandibular rami, an almost equal number of the corresponding element from the right side, two nearly complete skulls, and several fragmentary skulls. The mandibles are often noteworthy for their size, for they occasionally exceed the average of *M. c. æstuarinus* in this respect.

According to Kellogg (p. 1) this race of meadow mouse is semi-aquatic, and is limited in range to the San Joaquin Valley.

LEPORIDÆ

As at Rancho La Brea the McKittrick lagomorph assemblage is made up of the jack rabbit, *Lepus californicus*, the cottontail, *Sylvilagus auduboni*, and the brush rabbit, *Sylvilagus bachmani*. According to Dice (1925, pp. 126-129) the cottontail and jack rabbit from Rancho La Brea are to be referred to extinct subspecies. The subspecies of the McKittrick lagomorphs still inhabit the San Joaquin Valley.

The leporids present many difficulties to the palæontologist, and many questions which concern the McKittrick forms have not been answered. Dice (*op. cit.*, pp. 128-129, 1925) states that *Sylvilagus bachmani* can usually be distinguished from *Sylvilagus auduboni* by relative size of skull and complication of the enamel pattern of the cheek-teeth. The latter is stated to be larger in size than in the brush rabbit and to possess a more complicated enamel pattern. Owing to difficulty in fixing the age of an individual, these criteria are not very useful when dealing with a relatively small series. In addition, the McKittrick collection contains several specimens which while apparently adult and of approximately the same size as the brush rabbit possess a rather complicated enamel pattern; while a number of adult specimens of a size common to *Sylvilagus auduboni* show a very simple enamel pattern. Consequently, it is very difficult to make a satisfactory specific determination of each individual. It would appear, however, that the jack rabbit, the cottontail, and the brush rabbit are all represented in the McKittrick fauna.

As in the case of rodents, it appears that a large number of the McKittrick lagomorph specimens are of rather Recent age. The peculiar mode of occurrence of much of the McKittrick rabbit material (see page 130) makes this supposition even more plausible.

Lepus californicus Gray

No less than 41 individuals are represented by a series of left mandibular rami in the collections of the California Institute. In addition the collection contains several more or less complete skulls, right mandibular rami, and numerous other skeletal elements.

In general the material cannot be distinguished from *Lepus californicus richardsoni*, which inhabits the San Joaquin Valley at the present time. A few of the mandibles show a rather straight horizontal ramus and relatively long diastema. In this respect they correspond to *Lepus californicus orthognathus* from Rancho La Brea, and it is possible that two races of jack rabbit are present in the McKittrick fauna. On the other hand, when it is remembered that Dice's subspecies (1925, pp. 126-127) is based on a single mandible, its validity seems doubtful. In any event, retention of Dice's variety serves no useful purpose insofar as correlation and description of the two faunas are concerned and in this paper *Lepus californicus orthognathus* is considered as identical with at least the straight-jawed McKittrick jack rabbits referred to *Lepus californicus*. In view of geographic separation, however, it is probable that the McKittrick and Rancho La Brea forms belong to distinct subspecies, but until osteological differences between living varieties have been demonstrated no satisfactory separation can be made.

In view of the difficulty in distinguishing young individuals of this species from the *Sylvilagus* group no table of measurements of the McKittrick leporids is given.

Sylvilagus bachmani (Waterhouse)

At least 28 individuals are represented by left mandibular rami in the collections of the California Institute. The collection also contains several right mandibular rami and four rather imperfect skulls. All the adult material falls within the size range of the brush rabbit as contrasted with the cottontail, but the enamel pattern of the cheek-teeth is not always as

complicated as is the case in *Sylvilagus bachmani*. While the procedure is admittedly questionable, it has been thought best to refer all specimens which fall within the proper size range to *Sylvilagus bachmani* regardless of the degree of complication shown by the enamel pattern.

Sylvilagus auduboni (Baird)

The cottontail is apparently twice as abundant in the collections of the California Institute as is the brush rabbit. Fifty-four left mandibular rami are referred to this form, in addition to a large number of the corresponding element from the right side and several more or less complete skulls. While there is considerable variation in complication of the enamel pattern of the cheek-teeth, both in size and in proportions this material indicates a form not far removed from *Sylvilagus auduboni*.

SORICIDÆ

The McKittrick fauna contains a species of shrew very close to *Sorex ornatus*, a form which also occurs at Rancho La Brea and Carpinteria. It is possible that the McKittrick material is of Recent age, but since species of this family are unusually long-lived, the supposition is difficult to prove.

Sorex cf. ornatus (C. H. Merriam)

This form is represented by a left mandibular ramus, No. 2126 C.I.T., which apparently represents a young individual. This specimen lacks only P4 and M3. No. 2126 compares closely in size with No. C152, a juvenile female in the Dickey collection of Recent mammals. The only noteworthy differences between the McKittrick material and the Recent specimen are the more slender horizontal ramus and slightly larger teeth in the former. Since size is supposed to be a very constant character among these insectivores, it seems possible that the asphalt form represents a new subspecies.

The McKittrick specimen differs from *Notiosorex* in farther forward position of the premolars and in the position of the molars, M3 especially. These teeth are not so close to the median plane of the jaw and therefore do not permit the presence of a shelf along the outer border of the horizontal ramus.

The type from the asphalt differs from *Sorex obscurus obscurus* in greater length of lower middle incisors and in slightly shorter condyles.

In *Sorex trowbridgii trowbridgii* the lower middle incisors are somewhat shorter and project nearly straight forward, while in the McKittrick specimen these teeth are longer and possess a distinct upward curvature along their anterior extremities.

Sorex montereyensis montereyensis differs, among other characters, from the McKittrick form in its larger size.

Sorex californicus californicus is smaller than either of the McKittrick specimens; while *Sorex trowbridgii humboltensis* is much larger.

VESPERTILIONIDÆ

The McKittrick collection contains a bat, which as in the case of the shrew, may be Recent in age.

Antrozous pallidus pacificus C. H. Merriam

A single right mandibular ramus, No. 2127 C.I.T., is the only specimen available. Although the horizontal ramus is slightly deeper below the

cheek-teeth than is usual in the living species, there are few, if any, other important differences. P₃ is missing, but the alveolus and notch on the postero-internal border of the canine indicate that this tooth was of approximately the same size and shape as in the Recent form. P₄ has a slightly smaller heel and more nearly vertically directed principal cusp than a male specimen, No. C26, of the Dickey collection. These characters seem to be somewhat variable in the Recent material, however, for No. 15582, a female from the same collection, corresponds almost exactly to the McKittrick specimen in characters of the last lower premolar. Since no other differences between the fossil and living form are found, the McKittrick specimen is referred to *Antrozous pallidus pacificus*, a race which still inhabits the mountains bordering the San Joaquin Valley.

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FIG. 1—View of the McKittrick fossil quarry at an early stage of excavation.



FIG. 2—View of the McKittrick fossil quarry at a later stage of excavation showing one of the larger asphalt-filled pipes.



Smilodon californicus Bovard

FIGS. 1-1b—Skull, C.I.T. No. 650, lateral, occlusal, and dorsal views.

FIGS. 2, 2a—Right ramus of mandible, C.I.T. No. 650, lateral and occlusal views.

All figures approx. 1/4 nat. size.

Calif. Inst. Tech. Vert. Pale. Coll. Late Pleistocene, McKittrick, Calif.



Felis atrox Leidy

FIGS. 1-1b—Skull, C.I.T. No. 648, lateral, dorsal, and occlusal views.

FIGS. 2, 2a—Left ramus of mandible, C.I.T. No. 648, lateral and occlusal views.

All figures approx. $1/5$ nat. size.

Calif. Inst. Tech. Vert. Pale. Coll. Late Pleistocene, McKittrick, Calif.



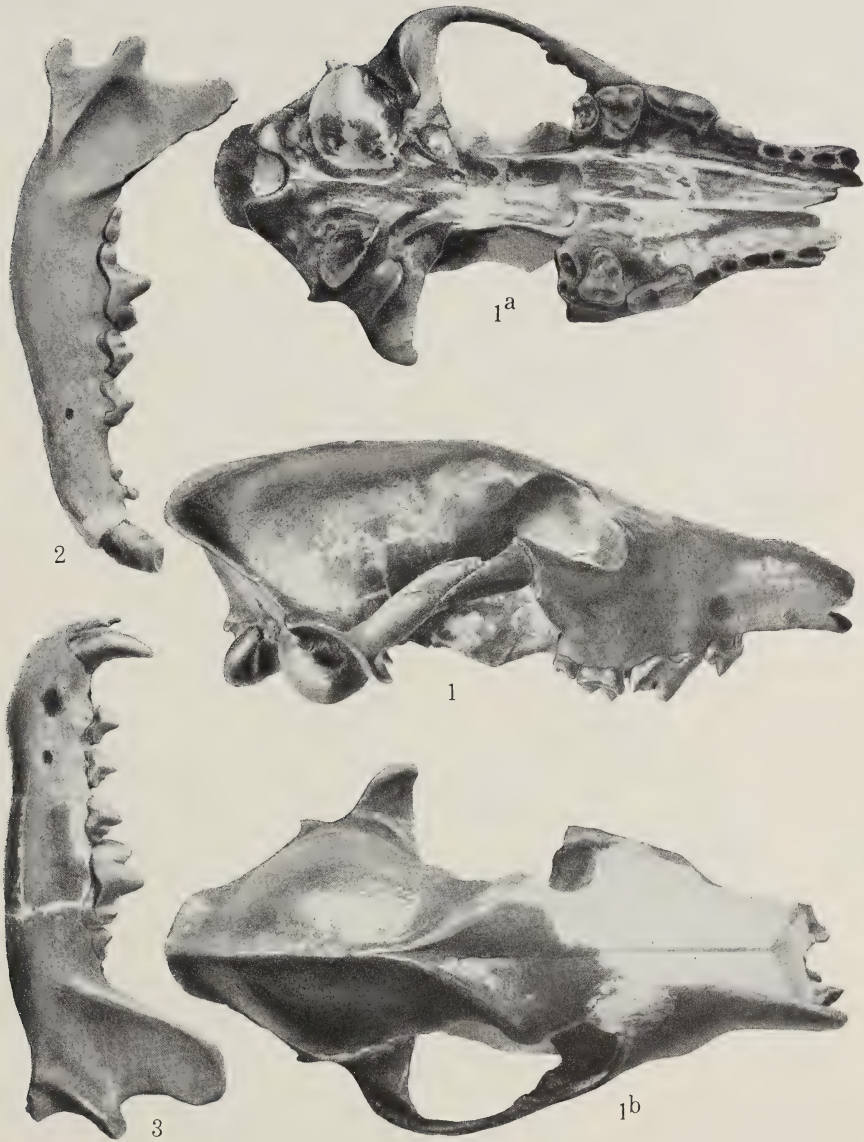
Felis daggetti Merriam and *Lynx rufa* cf. *fischeri* Merriam

FIGS. 1, 1a—*Felis daggetti*, skull, U.C. No. 29524, lateral and occlusal views.

FIGS. 2, 2a—*Lynx rufa* cf. *fischeri*, right ramus of mandible, C.I.T. No. 2040, lateral and occlusal views.

All figures approx. 3/5 nat. size.

Calif. Inst. Tech. and Univ. Calif. Vert. Pale. Coll. Late Pleistocene, McKittrick, Calif.



Canis latrans orcutti Merriam

FIGS. 1-1b—Skull, C.I.T. No. 2041, lateral, occlusal, and dorsal views.

FIG. 2—Right ramus of mandible, C.I.T. No. 2064, lateral view.

FIG. 3—Left ramus of mandible, C.I.T. No. 2068, lateral view.

All figures approx. 1/2 nat. size.

Calif. Inst. Tech. Vert. Pale. Coll. Late Pleistocene, McKittrick, Calif.



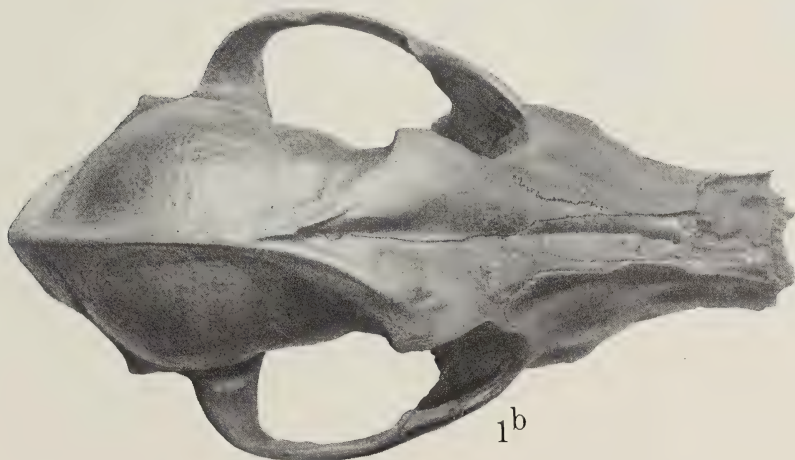
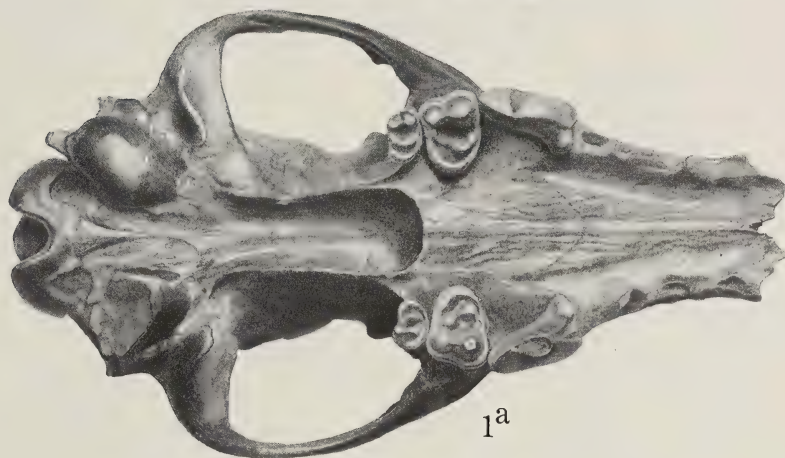
Canis latrans orcutti Merriam (*C. latrans*-like type)

FIGS. 1-1b—Skull, C.I.T. No. 2047, lateral, occlusal, and dorsal views.

FIG. 2—Left ramus of mandible, C.I.T. No. 2067, lateral view.

All figures approx. 1/2 nat. size.

Calif. Inst. Tech. Vert. Pale. Coll. Late Pleistocene, McKittrick, Calif.



Canis latrans orcutti Merriam

FIGS. 1-1b—Skull, C.I.T. No. 2046, lateral, occlusal, and dorsal views.

All figures approx. $\frac{3}{5}$ nat. size.

Calif. Inst. Tech. Vert. Pale. Coll. Late Pleistocene, McKittrick, Calif.



Enocyon dirus (Leidy) and *Enocyon* near *milleri* (Merriam)

FIGS. 1, 1a—*Enocyon dirus*, skull, C.I.T. No. 2077, lateral and occlusal views. Approx. $\times 1/3$.

FIGS. 2, 2a—*Enocyon dirus*, right ramus of mandible, C.I.T. No. 2081, lateral and occlusal views. Approx. $\times 2/3$.

FIG. 3—*Enocyon* near *milleri*, left M1, C.I.T. No. 2083. Approx. $\times 2/3$.

FIG. 4—*Enocyon* near *milleri*, right M1, C.I.T. No. 2082. Approx. $\times 2/3$.
Calif. Inst. Tech. Vert. Pale. Coll. Late Pleistocene, McKittrick, Calif.



Vulpes macrotis cf. *mutica* C. H. Merriam

FIGS. 1, 1a—Right ramus of mandible, C.I.T. No. 2086, lateral and occlusal views.
FIGS. 2, 2a—Skull, C.I.T. No. 2084, lateral and occlusal views.

All figures approx. nat. size.

Calif. Inst. Tech. Vert. Pale. Coll. Late Pleistocene, McKittrick, Calif.



Tremarctotherium simum (Cope)

FIGS. 1-1b—Skull, U.C. No. 33111, lateral, dorsal, and occlusal views.
FIG. 2—Right ramus of mandible, U.C. No. 33111, lateral view.

All figures approx. 1/5 nat. size.

Univ. of Calif. Vert. Pale. Coll. Late Pleistocene, McKittrick, Calif.



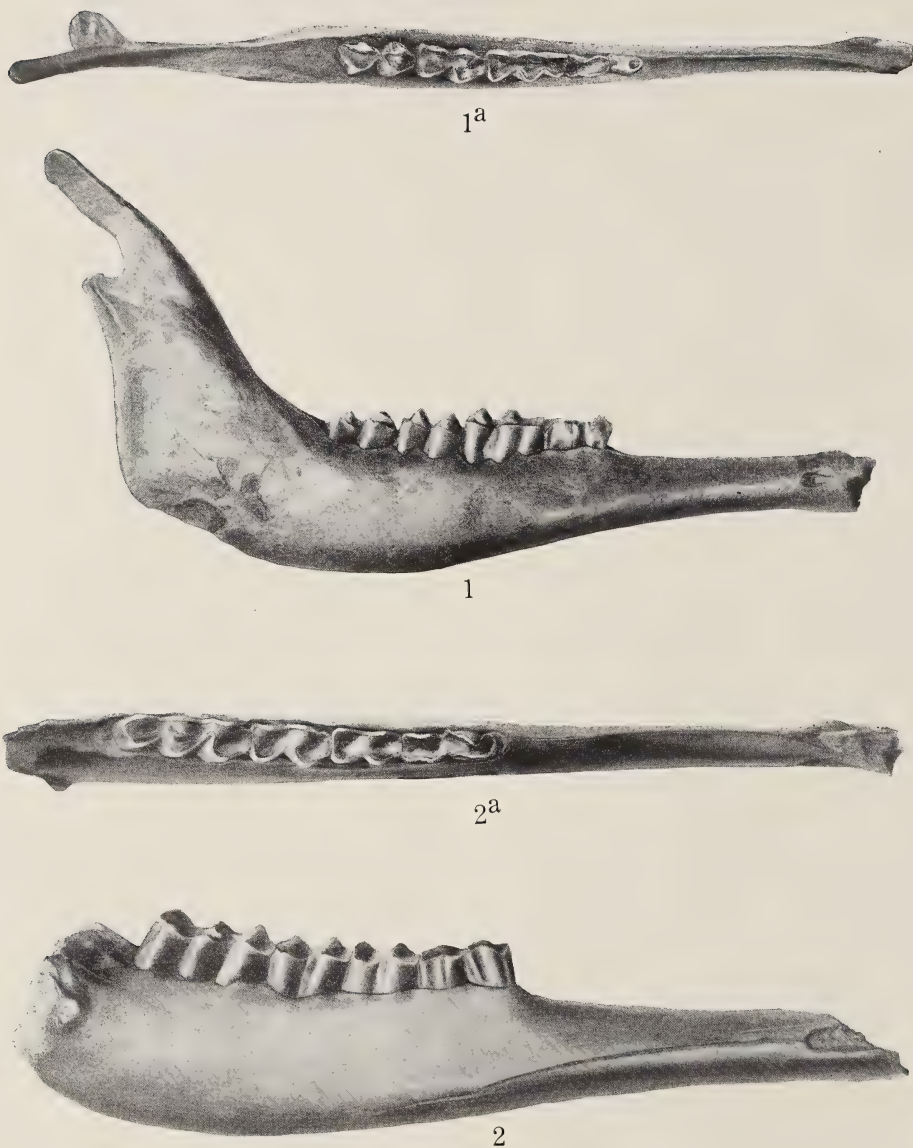
Ursus optimus n. sp.

FIGS. 1-1b—Skull, C.I.T. No. 2090, lateral, occlusal, and dorsal views.

FIG. 2—Left ramus of mandible, C.I.T. No. 2091, lateral view.

All figures approx. 1/3 nat. size.

Calif. Inst. Tech. Vert. Pale. Coll. Late Pleistocene, McKittrick, Calif.



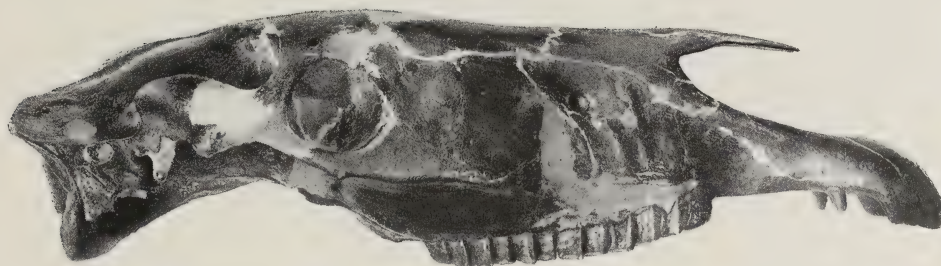
Antilocapra americana (Ord)

FIGS. 1, 1a—Right ramus of mandible, C.I.T. No. 2118, lateral and occlusal views. (Immature specimen with milk-teeth.)

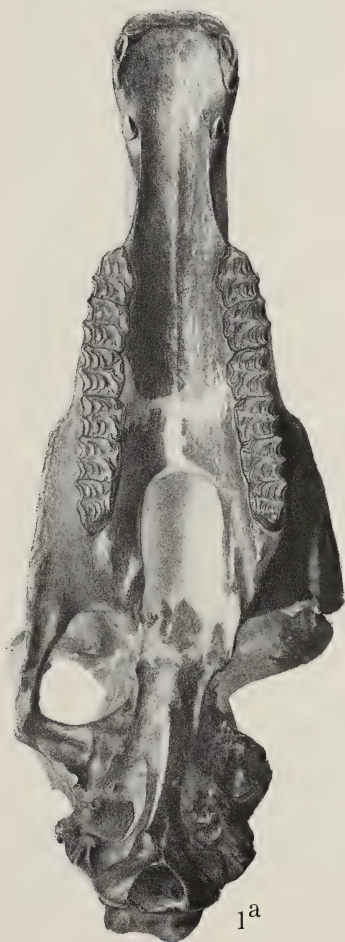
FIGS. 2, 2a—Right mandibular ramus, C.I.T. No. 2119, lateral and occlusal views. (Mature specimen.)

All figures approx. 2/3 nat. size.

Calif. Inst. Tech. Vert. Pale. Coll. Late Pleistocene, McKittrick, Calif.



1



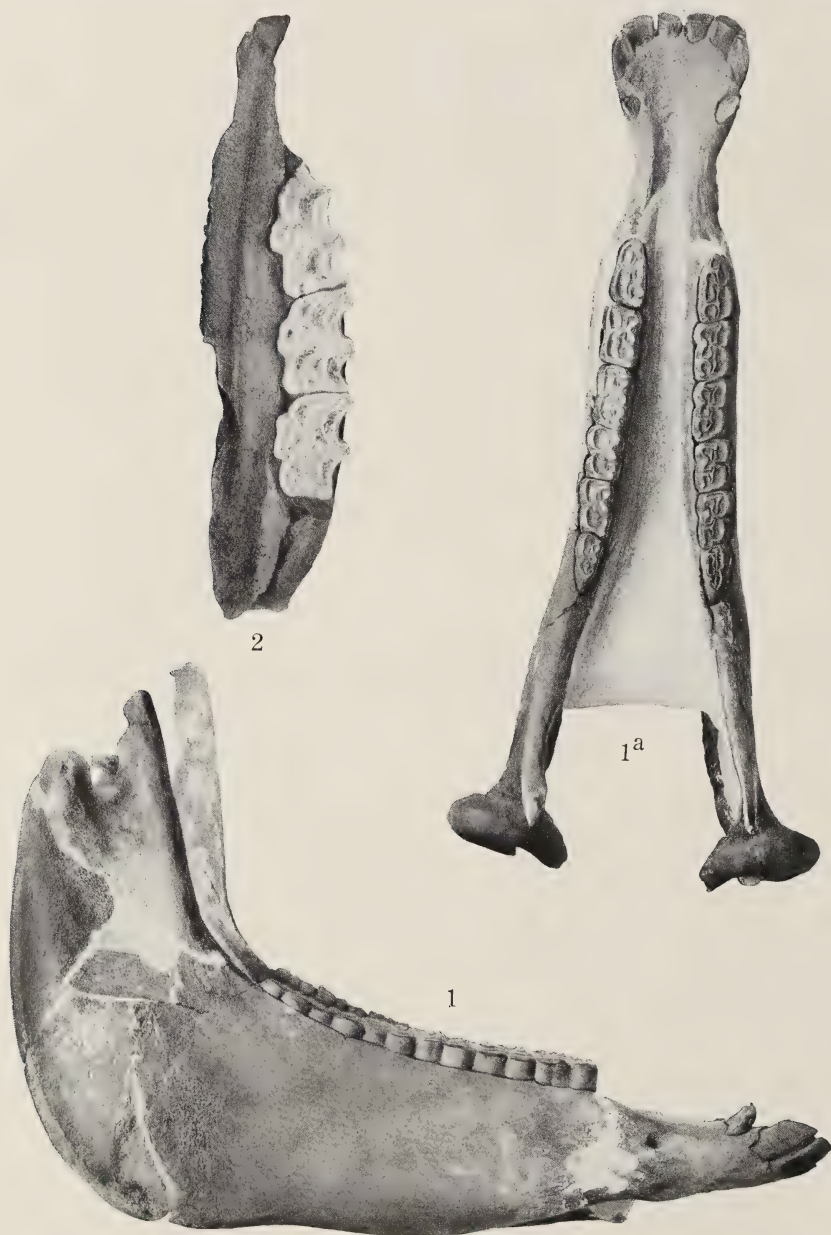
1^a



1^b

Equus occidentalis Leidy

FIGS. 1-1b—Skull, C.I.T. No. 1856, lateral, occlusal, and dorsal views. Approx. $\times 1/5$. Calif. Inst. Tech. Vert. Pale. Coll. Late Pleistocene, McKittrick, Calif.



Equus occidentalis Leidy

FIGS. 1, 1a—Mandible, C.I.T. No. 1855, lateral and occlusal views. Approx. $\times 1/4$.
 FIG. 2—Left maxillary fragment, C.I.T. No. 1862, containing Dm2-4. Approx. $\times 2/5$.
 Calif. Inst. Tech. Vert. Pale. Coll. Late Pleistocene, McKittrick, Calif.



Equus occidentalis Leidy and *Plesippus shoshonensis* Gidley

FIGS. A, B—*Plesippus shoshonensis*, pes and manus, C.I.T. No. 1863.

FIGS. C, D—*Equus occidentalis*, pes and manus, C.I.T. No. 2131, 2132.

All figures approx. 1/3 nat. size.

Calif. Inst. Tech. Vert. Pale. Coll. Late Pliocene, Hagerman, Idaho, and Late Pleistocene, McKittrick, Calif.



1



1^a

Parelephas columbi (Falconer)

FIGS. 1, 1a—M3, C.I.T. No. 2125, lateral and occlusal views. Approx. $\times 2/5$.
Calif. Inst. Tech. Vert. Pale. Coll. Late Pleistocene, McKittrick, Calif.



Mastodon raki Frick

FIG. 1—Right mandibular ramus containing Dm2-4, U.C. No. 22120, occlusal view. Approx. $\times 1/2$.

FIG. 2—M3, U.C. No. 33115, occlusal view. Approx. $\times 1/4$.

FIGS. 3, 3a—Right mandibular ramus containing M1-2, U.C. No. 33117, lateral and occlusal views. Approx. $\times 1/4$.

Univ. Calif. Vert. Pale. Coll. Late Pleistocene, McKittrick, Calif.

CONTRIBUTIONS TO PALÆONTOLOGY

V

THE RANCHO LA BREA CARACARA: A NEW SPECIES

BY HILDEGARDE HOWARD

With three plates and one chart

[Issued July 7, 1938]

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THE RANCHO LA BREA CARACARA: A NEW SPECIES

INTRODUCTION

In connection with curatorial duties at the Los Angeles Museum, I have had occasion from time to time to go over the bones of the Rancho La Brea caracara, at present listed as *Polyborus cheriway*. In so doing, certain peculiarities have become evident and I have come to question the status of the bird as now recorded.

The first mention of the caracara from Rancho La Brea was L. H. Miller's (1909, p. 306) record of "a small *Polyborus*" included in a list of birds then known from the asphalt deposit. In the next listing (L. H. Miller, 1912, pp. 78, 95, 114) it appeared as *Polyborus tharus*.¹ In 1925 the first discussion of the species was published and it was reclassified as *Polyborus cheriway* (L. H. Miller, 1925, pp. 99-101). This change was made on the basis of Ridgway's records (1875, p. 455) of the range in size of tarsi in *cheriway* as compared with *plancus*. At this time Miller studied a series of thirty-two tarsometatarsi of the Rancho La Brea bird in the Los Angeles Museum collections, and remarked: "The series shows a perfect intergradation in length between 83 and 94 mm., yet all the shorter specimens display a stockiness of form. The character alone is scarcely sufficient to prove the presence of two species yet the suggestion is a very positive one."

It is obvious, therefore, from Miller's work that he too felt there was something out of the ordinary about the Rancho La Brea caracara—the identification with *P. cheriway* being more or less a matter of giving it some name until the subject could be studied more completely.

Within the past year the opportunity has arisen to make a detailed and exhaustive study of the material. The purpose of this report is to present the data accumulated and the resulting conclusions.

MATERIAL AVAILABLE

Over nine hundred bones of the Rancho La Brea bird, in the collections of the Los Angeles Museum, have been examined. These represent well over one hundred and fifty individual birds. The skeletal elements studied in detail include the upper mandible (beak), coracoid, pelvis, humerus, ulna, carpometacarpus, femur, tibiotarsus, and tarsometatarsus. The cranium, lower mandible, furcula, scapula, sternum, and radius, being of little diagnostic value in this instance

¹ *Polyborus tharus* Molina 1782 = *Polyborus plancus* (J. F. Miller) 1777.

owing to the condition of the material, are not included in the discussion.

Comparative skeletal material at hand for constant scrutiny included the following specimens:

Species	Material	Collection
<i>Polyborus cheriway</i>		
specimens from U. S., Mexico, Central and South America	4 complete skeletons 1 complete, 1 incomplete skeleton 2 complete, 3 incomplete skeletons	U. S. Nat. Mus. Dr. Loye Miller L. A. Mus.
<i>Polyborus plancus</i>		
specimens from Argentina and Patagonia....	2 complete skeletons 1 complete skeleton 1 complete skeleton	U. S. Nat. Mus. Dr. Loye Miller L. A. Mus.
<i>Polyborus lutosus</i>		
Guadalupe Island	1 complete skeleton	U. S. Nat. Mus.
<i>Polyborus latebrosus</i> ¹		
Puerto Rico.....	Type carpometacarpus	Amer. Mus. Nat. Hist.

Modern skeletons of *P. cheriway* in the collections of the California Museum of Vertebrate Zoology were checked over for possible variations, but, being in all cases similar to the specimens on hand, were not borrowed for detailed study or measuring.

Bones previously identified as *Polyborus cheriway* from other fossil deposits were available, as follows:

Deposit	Material	Collection
McKittrick, Calif., Pleistocene.....	25 bones	Calif. Inst. Tech.
Carpinteria, Calif., Pleistocene.....	19 bones	Santa Barbara Mus.
Seminole Field and Melbourne, Fla., Pleistocene	14 bones	U. S. Nat. Mus.
Conkling Cavern, N. M., Pleistocene.....	6 bones	L. A. Mus.
Shelter Cave, N. M., Quaternary.....	1 bone	L. A. Mus.

ACKNOWLEDGMENTS

For placing at my disposal the comparative material above mentioned, I am indebted to Dr. Loye Miller, University of California at Los Angeles; Dr. Alexander Wetmore, United States National Museum; Dr. Chester Stock, California Institute of Technology; Dr. Joseph Grinnell, California Museum of Vertebrate Zoology; Mr. David Banks Rogers, Santa Barbara Museum of Natural History; Dr. Walter Granger and Mrs. Rachel Nichols, American Museum of Natural History.

¹ Described by Wetmore from a Puerto Rican cave of geologically Recent age. Type description 1920, pp. 77-78; reviewed with additional information 1922, pp. 303-306.

Through the courtesy of Dr. Clinton G. Abbott and Mr. Lawrence P. Huey, opportunity was afforded to examine skins of *Polyborus lutosus* in comparison with skins of *Polyborus cheriway* in the collections of the San Diego Museum of Natural History.

Skins of *Polyborus cheriway* were made available also through the kindness of Mr. George Willett, Los Angeles Museum, and Dr. Louis B. Bishop.

In addition to assistance rendered in the matter of loan of material, many of the above-named persons have further aided in the completion of this work by affording encouragement and helpful suggestions in some of the difficult aspects of the present problem.

The help of Mr. George Huston, in the matter of measuring specimens, is gratefully acknowledged.

The illustrations were prepared by John L. Ridgway from photographs by Dr. Richard Millar, Los Angeles Museum. The chart was drawn by Mr. David P. Willoughby.

DISCUSSION

The marked variability in characters of the individual skeletal elements has proved the greatest stumbling block in the matter of determining the proper status of the Rancho La Brea caracara bones. Although a certain amount of variation is encountered in the existing species of caracara, in most characters there is still sufficient hiatus between them to distinguish the elements of each. Among the asphalt bones, however, we find characteristics of all the other species. These occur so as to run one into the other, with no possibility of segregating the specimens into two or more distinct groups. Regarding the stoutness of the shorter tarsi as pointed out by Miller, I find that in a series of 271, though the slenderest bones are to be found among the longest specimens and the stoutest among the shortest specimens, there is a decided overlapping of long and short bones in the middle range of stoutness. Furthermore, certain "off size" bones in *cheriway* and *plancus* also exhibit the tendency to stoutness in the case of the short and slenderness in the case of the long specimens, indicating that this condition may be expected within any species in the caracara group.

In spite of the variability of the Rancho La Brea bird, when it is considered as a whole there are certain definite trends which can be pointed out as representing its general features. We have therefore no alternative but to accept the fossil bones as belonging to a single, extremely variable species.

Comparing the general features of the fossil first with *Polyborus cheriway*, since it is now assigned to that species, we find the following most important distinctions:

1. The greatest length attained in 271 specimens of the fossil tarso-metatarsus is 94.8 mm. This is 2.3 mm. below the maximum of the nine available tarsi of *cheriway*. Furthermore, of these nine tarsi of *cheriway*, five are larger than 94.8 mm. The same is true of the tibial length; the maximum of thirty-eight fossil tibiotarsi available for measurement is 112.3 mm., which is exceeded by all but two of ten specimens of *cheriway*.

2. Contrasting with the short tarsus and tibia of the fossil, the carpometacarpus goes to the opposite extreme. Sixty-seven fossil bones of this element exceed the maximum for *cheriway*, while none quite equals the minimum of that species. These comparisons may be more easily visualized by consulting the accompanying chart.

3. The beak is broader, shorter, and lower in the fossil, and the line at the bridge is more posteriorly located with respect to the nares.

4. In the humerus, (a) the outline of the bicipital crest tends to be a well-rounded curve, with its outermost extent slightly distal to the mid-point of this curve, while in *cheriway* the outline is more angular and the "apex" is proximal to the mid-point, with the crest straightening out below this "apex"; (b) the ectepicondylar prominence is more angular and more prominent in the fossil.

5. In the carpometacarpus, (a) there is present a crest formed by the internal edge of the trochlea, and emphasized by a slight excavation above the pisiform process; the crest and excavation are absent, or nearly so, in *cheriway*; (b) a marked excavation of the internal side beneath the pisiform process in the fossil is absent in *cheriway*.

6. The internal side of the tarsometatarsus in the fossil is markedly furrowed and its posterior outline tends to be angular. In *cheriway* the furrow is replaced by a slight depression near the posterior edge, and this edge is curved, not angular.

Comparison of the fossil caracara with *Polyborus plancus* shows considerably greater similarity than with *cheriway*. However, the maximum length of each element of *plancus* so far exceeds the maximum of the asphalt specimens that there can be no possibility of identity. Other points which indicate nonidentity of these forms are:

LEGEND TO CHART ON PAGE 223

Chart comparing the size distribution of each of the limb elements and the coracoid, of the various species of caracara.

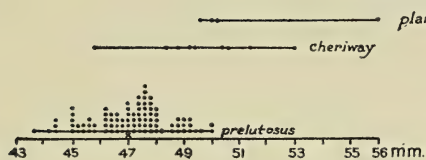
Dots indicate individual bones; connecting lines mark the range in size for each species.¹

Measurements of the one available skeleton of *lutusus* are indicated by cross marks placed immediately adjacent to the fossil graphs for ease of comparison.

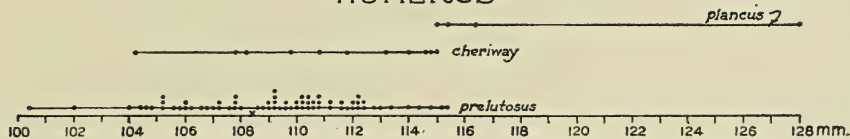
Numbers denote length of elements in millimeters.

¹The range in the femur of *prelutosus* should reach 72.8 mm., to include an additional specimen measured since chart was drawn.

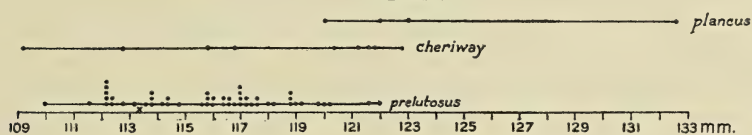
CORACOID



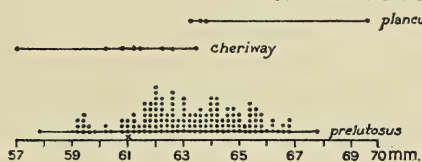
HUMERUS



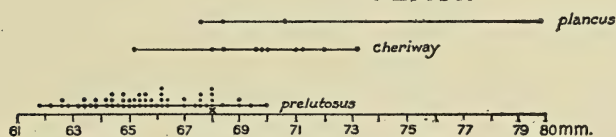
ULNA



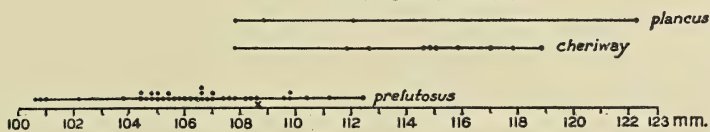
CARPOMETACARPUS



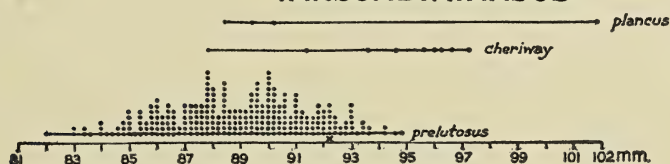
FEMUR



TIBIOTARSUS



TARSOMETATARSUS



x, in each of the above graphs = measurement of lutosus
(For legend to chart, see page 222, bottom)

1. In proportions of many of the individual elements, the fossil overlaps both the stout bones of *plancus* and the slender bones of *cheriway*.

2. The resemblance of the fossil to *plancus* in certain individuals, grading off into dissimilarity in others, is noted also in many physical characters. The most important of these are: (a) The straight femur, with broad, smooth flare of the trochanteric area, characteristic of *plancus*, is approximated in a few fossil individuals, while others vary in greater rugosity, or greater curvature, or diminished trochanteric flare. (b) In the humerus, certain individuals have the broad, short bicipital crest as in *plancus*, while in others the crest is extended farther distally. (c) In the carpometacarpus, some fossil individuals resemble *plancus* in the very slight development of the trochlea inward in the form of a crest; others have this crest well developed. (d) The area distal to the pisiform process in the carpometacarpus is similar to that of *plancus* in a few fossil individuals, though the majority are more markedly excavated than in any of the other species studied, including *latebrosus*.

Both in size and in physical characters the fossil is close to *Polyborus lutosus*. Unfortunately, only the one skeleton of this species has been preserved, so that nothing can be said of the variability of its skeletal elements. Ridgway, in describing the plumage of the bird, says (1875, p. 460): "In both adult and immature stages there is considerable variation, but all within the limits of the above diagnosis." His diagnosis shows the bird to be easily distinguishable from both *cheriway* and *plancus*, though with closer affinity to the latter. Comparison of the skeleton, also, shows greater similarity to *plancus*, though in the matter of proportions of the leg to the wing bones, *lutosus* has the relatively longer legs characteristic of *cheriway*.

Lacking additional specimens of *lutosus* with which to determine its trend of variation, the fact that certain fossil individuals resemble *lutosus*, while others range off to overlap other species, is not alone as convincing evidence of distinction as in the case of *cheriway* or *plancus*. It is noteworthy, however, that, in other respects than that of size, many of the fossil bones agree with *plancus* as readily as, and in certain proportions even more readily than, with *lutosus*. Still more significant is the fact that a few characters peculiar to *lutosus* are unrepresented throughout the great range of variability of the Pleistocene form. These characters are as follows:

1. In the humerus of *lutosus*, the pneumatic fossa opens from a large pneumatic foramen, with floor "dished out" and depressed to the level of the bicipital crest; in the fossil the fossa is at a noticeably higher level than the crest, with a step from one to the other in most

specimens; a single fossil specimen approaches *lutosus* in level but is not "dished out" (see plate 1).

2. In the pelvis, the most diagnostic character is found in the proportion of breadth to length of the renal cavity. In this respect the fossil agrees with *plancus* in great breadth of the cavity; *lutosus* falls with *cheriway*, being narrower.

3. In proportions of length of leg to length of wing bones, where, as I have indicated, *lutosus* resembles *cheriway*, the fossil is closer to *plancus*. I am fully aware of the difficulty of accurately comparing proportions when dealing with a fossil form in which there is absolutely no association of elements by individuals. In order to ascertain how closely one may approach the condition of actually associated elements in a random series, I have compared results with unassociated specimens of *cheriway*. In *cheriway* the unassociated bones, in which maximums were all placed together, minimums likewise, and then means and finally medians, showed less range of variation in the resulting ratios than when individual birds were considered (ratios of length of leg to length of wing for unassociated specimens, 95.6 to 96.2 per cent; for individual birds, 94.6 to 97.3 per cent). Ratios obtained from fifty each of fossil leg and wing bones range from 89.7 to 91.6 per cent. Allowing another 2 per cent at each extreme should, I believe, provide a fair estimate of the range for individual birds. With this addition the ratios for the fossil vary from 87.7 to 93.6 per cent. In *lutosus* the ratio is 95.1 per cent, and in *plancus* 87.8 to 92.0 per cent.

As further proof of the actual difference in proportion of leg to wing length in the fossil as compared with *lutosus*, the graphs in the accompanying chart show the position of *lutosus* relative to a series of each element of the leg and wing in the fossil. It is obvious from these graphs that though *lutosus* falls near the median with respect to body size (as represented by the coracoid) in the ulna and carpometacarpus, it falls well toward the minimum for the fossil, and in the femur, tibiotarsus, and tarsometatarsus it falls well toward the maximum.

In view of these differences, and the many characters of the fossil which overlap *plancus* and *cheriway*, I believe the fossil to be distinct from *lutosus* as well as from the two living species.

Comparison of the fossil with *latebrosus* reveals marked overlapping similarities. However, the unusual position of the notch between the process of metacarpal 1 and the trochlea separates *latebrosus* from the Rancho La Brea bird, as well as from all the other species.

The Rancho La Brea species, being distinguishable from all the other known caracaras, is therefore here designated as a "new" species.

In a case of this kind where series of several skeletal elements have been taken into consideration in drawing a conclusion, it is a problem

to select a single specimen of a single element to set up as the type of the new species. One element may best display the differences from one species, another is more diagnostic with respect to a second species. Or, having decided upon an element, it is difficult to choose a single typical specimen from so variable a series. As it is of greatest importance to bring out the differences as compared with *lutosus*, the humerus has been chosen as the element best suited for this purpose. The specimen selected is near the average for the fossil. It can be readily understood that the description of this so-called type does not in any measure suffice as descriptive of the species as a whole. Comparative descriptions based upon series of each element are therefore provided in addition.

DESCRIPTION OF SPECIES

Polyborus prelutosus, n. sp.

Type—Right humerus, L. A. Mus. No. E4398, from Pit 4, Rancho La Brea, Los Angeles, California; Pleistocene.

Diagnosis of type—(1) Outline of bicipital crest (palmar view) intermediate between *cheriway* and *plancus*, slightly more angular than the latter, but more curved and with point of greatest extent of curvature lower than in the former, though not so low as in *lutosus*. (2) Area of pneumatic fossa (ulnar view) markedly set up from the bicipital crest with definite "step" between, contrasting with decidedly "dished out" condition of the area in *lutosus*. (3) Ectepicondylar prominence a well-marked, sharp-pointed protuberance, closest to *lutosus* but even more sharply pointed and more proximally extended than in that species; palmar side distal to the protuberance, raised into a small, sharp ridge, found in none of the previously named forms. See plate 1, fig. 1 and plate 2, fig. 3 for illustration of type specimen.

Description of assigned material—As a matter of convenience in comparison, the descriptions of series of other elements of the skeleton and other individuals of the type element are presented in tabular form. See pages 228–236. The fossil elements are represented in the following numbers: beak 6, coracoid 90, humerus 69, ulna 52, carpometacarpus 151, pelvis 14, femur 56, tibiotarsus 38, tarsometatarsus 271. In many measurements, however, fewer specimens are represented, as the areas to be measured are, of course, not equally well preserved on all the bones.

In three elements, the coracoid, ulna, and pelvis, the differences between the species can be noted only in the proportions of the bone. Diagnostic characters of the other elements (other than measurements) vary from one in the tibiotarsus to seven in the carpometacarpus. In each character the general trend of the majority of specimens is given for the fossil, with mention of the variation included in its range.

In the tarsometatarsus, measurements of length are given for skins as well as for the skeletons available. The skin measurements were estimated from specimens listed in Ridgway, 1875, pp. 457–461; 1915, p. 254; Bryant,

1887, p. 283; Friedmann, MS.; Sharpe, 1874, pp. 31-33; and from measurements taken personally on skins in the collections of the San Diego Museum, Dr. Louis B. Bishop, and the Los Angeles Museum. In *P. cheriway* considerable difference is noted between skin and skeletal measurements, the latter running somewhat larger.

Size difference between the northern and southern races of *Polyborus cheriway* is not apparent in the tarsal length. Among the skeletons, both the shortest and the longest available specimens come from Mexico. Of the elements present in the incomplete skeleton of the South American specimen, only the carpometacarpus (of which the proximal end alone is present) appears smaller than the smallest of the northern specimens.

In studying the tables the average trend of the fossil should be given particular consideration. In size this average shows *prelutosus* to be smaller than either *cheriway* or *plancus*, with leg bones and beak even smaller than *lutosus*.

The most outstanding characters of the fossil are found in (1) the small, though relatively broad beak with short distance from naris to ramus; (2) the well-developed ectepicondylar process of the humerus with accompanying ridge distal thereto; (3) the large carpometacarpus, well excavated around the pisiform process and with external trochlea equally well extended at two points on its posterior rim; and (4) the relatively broad pelvis with broad renal cavity.

Other characters are of importance in comparison with one species but not with another, and in instances of marked overlapping, only a few specimens of an element may be identifiable. It may be seen, therefore, that the possibility of identifying isolated fossil caracara bones depends not only upon finding a characteristic element, but upon the individual specimen itself being diagnostic. Fortunately, in Quaternary deposits of the United States, *cheriway* is the one other species likely to occur, and it is also the most easily distinguished from *prelutosus*. In addition to the characters mentioned in the above paragraph and those enumerated on page 222, the tables show certain differences between the fossil and *cheriway* in the proportions of the coracoid, in the breadth of the shaft of the ulna, and in the point of greatest depth of the internal side of the shaft of the tarsometatarsus. About half of the tarsometatarsi also differ from *cheriway* in the position of the distal foramina on the posterior side.

UPPER MANDIBLE (BEAK)
(Plate 3, figures 1, 2)

	<i>P. cheriway</i>	<i>P. plancus</i>	<i>P. lutosus</i>	<i>P. prelutosus</i>
Position of lines bordering cere (one at bridge; other from naris to edge of ramus)	Both approximately even with anterior border of naris; upper line (across bridge) well anterior to septum of naris; lower line extending nearly straight to ramal edge from below naris	Both farther posterior with respect to naris; upper line directly over septum or very slightly anterior thereto; lower line slanting well posteriorly to ramal edge from below naris	Similar in position to those of <i>plancus</i> , except upper one posterior to septum of naris	Similar in position to those of <i>plancus</i> and <i>lutosus</i> ; upper one varies in different individuals, some slightly anterior to septum, some even with septum, and others posterior thereto
Shape of nares	Tend to be long, narrow, and slitlike; upper and lower parts approximately equal in breadth	Tend to be broader and shorter; lower part broader than upper; slight crook between upper and lower parts eliminates slitlike appearance of <i>cheriway</i>	Similar to <i>plancus</i> , though probably even broader	Tend to be short and to have crook between upper and lower parts; most are broader at lower part, but some are the same breadth in each portion, as in <i>cheriway</i>
Length of beak from curve of ramus near tip to top of naris	26.3-29.5 mm.	24.8-27.1 mm.	24.5 mm.	21.6-23.9 mm.
Breadth of beak below nares	12.5-13.6 mm.	13.9-15.1 mm.	15.1 mm.	13.0-14.8 mm.
Height of beak at cere	16.5-17.3 mm.	15.6-17.8 mm.	16.0 mm.	14.4-15.0 mm.
Distance from lower edge of naris to ramus	10.5-11.3 mm.	10.2-10.6 mm.	9.3 mm.	7.6- 8.8 mm.
Ratio of breadth to length	to 45.0-49.5 per cent	55.7-57.9 per cent	61.6 per cent	58.1-67.6 per cent
Ratio of breadth to height	to 73.0-79.1 per cent	84.9-93.0 per cent	94.4 per cent	90.3-101.4 per cent

CORACOID (RIGHT *)

	<i>P. cheriway</i>	<i>P. plancus</i>	<i>P. lutosus</i>	<i>P. pretulosus</i>
Length from internal tip to head	45.8-53.0 mm. (49.7 mm. mean)	49.3-55.9 mm. (51.2 mm. mean)	46.9 mm.	43.6-50.0 mm. (47.0 mm. mean)
Length of proximal part from scapular facet to head	17.3-19.3 mm.	19.5-21.6 mm.	17.5 mm.	17.2-19.0 mm.
Least depth of head	2.1- 2.5 mm.	3.2- 4.1 mm.	2.4 mm.	2.0- 3.3 mm.
Distance from foramen to scapular facet	8.3- 9.6 mm. 37.2-38.3 per cent	7.9- 9.7 mm.	8.7 mm.	6.4- 8.9 mm.
Ratio of length of proximal part to total length		38.6-39.9 per cent	37.3 per cent	36.6-41.2 per cent (half of specimens lower than <i>planicus</i>)
Ratio of least depth of head to total length	4.5- 4.9 per cent	5.7- 8.1 per cent	5.1 per cent	4.7- 7.0 per cent (only 2 out of 100 specimens agree with <i>cheriway</i> ; over half fall within <i>planicus</i>)
Ratio of distance from foramen to scapular facet to length of proximal portion	45.6-52.2 per cent	39.5-45.1 per cent	49.6 per cent	35.8-49.1 per cent (only 1 specimen out of 100 attains the maximum ratio; majority fall within <i>planicus</i> , or lower)

* Left coracoids have approximately 2 per cent greater length.

HUMERUS (Plates 1, 2)

	<i>P. cheriway</i>	<i>P. plancus</i>	<i>P. lutosus</i>	<i>P. prelutosus</i>
Contour of bicapital crest (palmar view) (see plate 2)	Angular in outline with "apex" at point of infraspinatus scar; continuing from this point in nearly straight line to end below the intermuscular line bordering the bicipital surface	Broadly rounded. No definite "apex," but point of greatest bulge of curve distal to infraspinatus scar; proceeding thence to round into shaft at, or only slightly below, the intermuscular line	Similar to <i>planus</i> , though with point of greatest bulge of curve even farther distally	Generally intermediate between <i>cheriway</i> and <i>planus</i> —moderately broad, rounded, with point of greatest extent of curve distal to infraspinatus scar; curving to join shaft below intermuscular line. Range includes overlapping <i>planus</i> , and close approach to <i>cheriway</i> , though none is identical with that species. In none is the greatest bulge as distal in position as in <i>lutosus</i>
Pneumatic fossa (see plate 1)	Level of fossa above that of bicipital crest, grading down gradually or with slight "step"	Level of fossa varying from above crest with "step," to almost level with the crest, with only a faint dividing line between crest and fossa	Fossa "dished out" to level of crest; this depression grades up into the shaft also	Fossa above crest in level. Most specimens agree with type in having "step," from fossa to crest, though some merge more gradually. Range overlaps <i>planus</i> and <i>cheriway</i> . One specimen approaches <i>lutosus</i> in level but is not "dished out"
Ectepicondylar process of distal end	Process and area distal thereto rounded and heavy looking. Process usually underdeveloped	Process angular and fairly prominent	Process appears more prominent than <i>planus</i> by reason of greater irregularity of external edge distal thereto; otherwise similar to <i>planus</i>	Well-marked, upward-projecting protuberance of type is characteristic of all other specimens in which process is intact. Ridge distal to process (characteristic of type and absent in all other species) may be so short as to be no more than a tubercle or may extend distally, to the condyle. The roundness or sharpness of the ridge varies also. In a few individuals it is absent entirely.

HUMERUS (continued)

	<i>P. cheriway</i>	<i>P. plancus</i>	<i>P. lutosus</i>	<i>P. prelutosus</i>
Greatest length	104.2-115.0 mm. (111.3 mm. mean)	115.0-128.0 mm. (118.6 mm. mean)	108.4 mm.	100.3-115.3 mm. (109.1 mm. mean)
Breadth of proximal end	20.9- 23.2 mm.	23.6- 25.3 mm.	22.3 mm.	20.5- 23.2 mm.
Breadth of distal end	17.3- 18.7 mm.	18.5- 20.6 mm.	18.5 mm.	17.0- 19.6 mm.
Ratio breadth of proximal end to length	19.1- 20.4 per cent (19.8 per cent mean)	19.7- 21.0 per cent (20.5 per cent mean)	20.5 per cent	19.2- 20.6 per cent (20.0 per cent mean)
Ratio breadth of distal end to length	15.5- 16.7 per cent (16.0 per cent mean)	16.1- 17.3 per cent (16.6 per cent mean)	17.0 per cent	16.3- 17.4 per cent (16.8 per cent mean)

ULNA

	<i>P. cheriway</i>	<i>P. plancus</i>	<i>P. lutosus</i>	<i>P. prelutosus</i>
Length	109.1-122.8 mm. (117.9 mm. mean)	119.9-132.5 mm. (124.3 mm. mean)	113.3 mm.	109.9-122.3 mm. (116.0 mm. mean)
Breadth of proximal end taken diagonally	13.9- 14.9 mm.	15.6- 16.7 mm.	15.5 mm.	14.1- 16.3 mm.
Breadth of distal trochlea	7.3- 8.2 mm.	8.6- 9.1 mm.	7.7 mm.	7.4- 8.7 mm.
Breadth of shaft at middle	4.8- 5.2 mm.	5.7- 6.3 mm.	5.7 mm.	5.0- 6.1 mm.
Ratio breadth of proximal end to length	11.9- 12.9 per cent	12.5- 13.7 per cent	13.6 per cent	12.3- 13.4 per cent (over half the specimens fall within the range of <i>cheriway</i>)
Ratio breadth of distal trochlea to length	6.5- 6.8 per cent	6.5- 7.4 per cent (all but the minimum are over 7.0 per cent; minimum is longest specimen)	6.8 per cent	6.4- 7.2 per cent (half the specimens are under 6.8 per cent)
Ratio breadth of shaft to length	4.2- 4.4 per cent	4.6- 5.1 per cent	5.0 per cent	4.4- 5.1 per cent (only 2 specimens out of 50 fall below 4.7 per cent)

CARPOMETACARPUS
(Plate 3, figures 3-5)

	<i>P. cheriway</i>	<i>P. plancus</i>	<i>P. lutosus</i>	<i>P. latebrosus</i>	<i>P. prelutosus</i>
Inward extension of antero-internal edge of trochlea to form crest	Absent or only faintly indicated	Generally better developed than in <i>cheriway</i> , but some bones overlap	Clearly marked	Decidedly marked	In most individuals fairly well developed (about intermediate between <i>plancus</i> and <i>lutosus</i>), ranging, however, from the faintly indicated crest of some bones of <i>cheriway</i> to the clearly marked crest of <i>lutosus</i> . None is as well developed as in <i>latebrosus</i>
Area between pisiform and trochlea	Unexcavated except a few specimens which have slight excavation just below trochlea; area occupied by a ridgelike convexity	More excavated than in <i>cheriway</i> especially anteriorly, adjacent to trochlea; convexity present but less developed than in <i>cheriway</i>	Well excavated particularly anteriorly, though convexity still present in a reduced state	Well excavated throughout; convexity absent except immediately adjacent to pisiform	Most individuals intermediate between <i>lutosus</i> and <i>latebrosus</i> in excavation, but with added deep excavation running distally anterior to pisiform. Range overlaps <i>plancus</i> , <i>lutosus</i> , and <i>latebrosus</i>
Under side of pisiform process and area distal thereto	Practically unexcavated (except on under side of pisiform in 2 specimens)	Slightly more excavated than in <i>cheriway</i>	Markedly excavated both under the pisiform and distal thereto	Similar to <i>lutosus</i> or slightly less excavated	Ranging from 3 bones which are near <i>cheriway</i> , to 40 which are more deeply excavated than all other species. Even the 50-odd specimens between these extremes have greater excavation on under side of pisiform than in other species, though area distal to pisiform overlaps in character
Posterior contour of external crest of trochlea	Greatest extent at distal edge	Greatest extent proximal to distal edge	Same as <i>plancus</i>	This portion of bone broken	Most specimens with both points equally developed. A few approach <i>cheriway</i> , a few others are like <i>plancus</i> and <i>lutosus</i>

CARPOMETACARPUS (continued)

	<i>P. cheriway</i>	<i>P. plancus</i>	<i>P. lutosus</i>	<i>P. latebrosus</i>	<i>P. prelutosus</i>
Process of metacarpal 1	Curved inward	Curved inward	Curved inward	Nearly straight	Most specimens curved inward, though some straight
Notch between processes of metacarpal 1 and trochlea	Anterior to junction of metacarpal 1 and trochlea	Same as <i>cheriway</i>	Same as <i>cheriway</i>	At the junction of metacarpal 1 and the trochlea	Same as <i>cheriway</i> , <i>plancus</i> , and <i>lutosus</i>
Proximal part of metacarpal 3	Flat or convex	Flat or convex	Flat or convex	Slightly depressed	A few specimens depressed, most are flat or convex
Length to anterior surface of distal end	57.0-63.4 mm. (61.1 mm. mean)	63.1-69.5 mm. (64.9 mm. mean)	61.0 mm.	Specimen incomplete	57.8-67.8 mm. (63.1 mm. mean)
Depth of proximal end (internal side)	14.6-16.2 mm.	16.0-17.4 mm.	15.5 mm.	16.0 mm.	14.6-17.0 mm.
Breadth of trochlea	5.7- 6.3 mm.	6.4- 7.2 mm.	6.4 mm.	6.6 mm.	5.5- 6.6 mm.
Ratio breadth of trochlea to depth of proximal end	37.0-40.6 per cent	39.0-41.4 per cent	41.3 per cent	41.2 per cent	35.6-42.7 per cent (64 out of 75 bones fall between 37.0 and 40.0 per cent, with 5 below 37 per cent and 4 above 40 per cent)

PELVIS

	<i>P. cheriway</i>	<i>P. plancus</i>	<i>P. lutosus</i>	<i>P. prelutosus</i>
Length of vertebral portion	53.6-60.8 mm.	58.5-65.2 mm.	57.8 mm.	53.8-61.1 mm.
Ratio of breadth above antitrochanters to length of vertebrae	59.4-66.7 per cent	61.9-71.4 per cent	66.3 per cent	66.8-75.0 per cent
Ratio of greatest breadth of renal cavity to length of renal cavity	83.2-95.5 per cent	89.1-100.2 per cent	86.9 per cent	90.8-104.8 per cent

FEMUR
(Plate 3, figures 6-9)

	<i>P. cheriway</i>	<i>P. planicus</i>	<i>P. lutosus</i>	<i>P. prelutosus</i>
Curvature	Bone appears curved; emphasized by general inward curving of proximal end (both internal and external contours) and of apex of posterior side of shaft proximally	Bone appears straight; emphasized by outward flaring of external contour, proximally (balancing inward slant of internal contour), and more vertical position of apex of posterior side of shaft	Bone appears straight; external contour of proximal end straight except for protruded distal edge of trochanter; apex of posterior side of shaft vertical in position	In general, bones appear straight with external contour of proximal end straight or slightly flaring, and apex of posterior surface of shaft vertical in position. Range also includes greater curvature, however
Rugosity of posterior and external surfaces of proximal end	Slightly rugose externally; obturator ridge usually well indicated, but not sharp (a few smooth)	Smoothen than <i>cheriway</i> externally; obturator ridge generally less marked than in <i>cheriway</i> , though one bone sharper	External surface decidedly rugose; obturator ridge very prominent and sharp	Generally slightly rugose, about as in <i>cheriway</i> ; obturator ridge also generally developed about as in <i>cheriway</i> , or a little more sharply. Range includes both smoother and more rugose specimens, however
Length (along internal side)	65.2-73.2 mm. (69.8 mm. mean)	67.6-79.8 mm. (71.5 mm. mean)	67.9 mm.	61.7-72.8 mm. (65.5 mm. mean)
Breadth of proximal end across greatest extent of trochanter	15.3-16.9 mm.	17.2-19.8 mm.	17.0 mm.	14.5-18.0 mm.
Breadth of distal end below process of fibular condyle	14.6-15.3 mm.	15.7-17.3 mm.	15.8 mm.	13.2-16.4 mm.
Breadth of shaft at middle	7.0- 7.4 mm.	7.6- 8.2 mm.	7.7 mm.	6.5- 8.0 mm.
Ratio breadth of proximal end to length	22.9-24.2 per cent	24.8-26.6 per cent	25.0 per cent	23.0-27.1 per cent (over half within <i>planicus</i>)
Ratio breadth of distal end to length	21.2-22.6* per cent (*shortest bone; other specimens under 21.8 per cent)	21.6*-23.6 per cent (*longest bone; others over 23.0 per cent)	23.2 per cent	20.0-24.1 per cent (over half within <i>planicus</i> or higher)
Ratio breadth of shaft to length	10.0-11.2* per cent (*shortest bone; others under 10.8 per cent)	10.2*-11.3 per cent (*longest bone; others over 11.0 per cent)	11.3 per cent	10.0-12.5 per cent (over half above 11.0 per cent)

TIBIOTARSUS

	<i>P. cheriway</i>	<i>P. plancus</i>	<i>P. lutosus</i>	<i>P. prelutosus</i>
Area immediately below articular surface, posteriorly only	Excavated above and internal to tubercle, with ridges bordering excavation	Area unexcavated; ridging absent or only faintly indicated	Same as <i>plancus</i>	15 specimens unexcavated and without ridges; 18 with faint ridging and no excavation; 6 faintly excavated and faintly ridged
Length to articular surface	107.7-118.8 mm. (114.5 mm. mean)	107.8-122.1 mm. (112.6 mm. mean)	108.6 mm.	100.5-112.3 mm. (106.2 mm. mean)
Breadth of proximal end	12.3-12.9 mm.	13.2-14.5 mm.	13.5 mm.	11.7-13.0 mm.
Breadth of distal end	13.0-13.8 mm.	13.5-14.9 mm.	13.7 mm.	12.2-13.8 mm.
Least breadth of shaft, distal to fibular spine	6.1-6.5 mm.	6.8-7.7 mm.	6.6 mm.	6.2-6.9 mm.
Ratio of breadth of proximal end to length	10.8-11.8 per cent	11.8-12.8 per cent	12.5 per cent	11.0-12.0 per cent (specimens equally distributed between <i>cheriway</i> and <i>plancus</i>)
Ratio of breadth of distal end to length	11.2-12.1 per cent	12.2-12.7 per cent	12.6 per cent	11.4-12.6 per cent (less than half the specimens fall within <i>cheriway</i>)
Ratio of breadth of shaft to breadth of distal end	45.3-47.7 per cent	50.0-52.2 per cent	48.2 per cent	47.5-53.0 per cent

TARSOMETATARSUS

(Plate 3, figures 10-12)

	<i>P. cheriway</i>	<i>P. plancus</i>	<i>P. lutosus</i>	<i>P. prelutosus</i>
Internal side of shaft	Faintly depressed, along posterior edge only. Posterior contour more rounded than angular, with point of greatest depth 10 to 15 mm. below tip of calcaneum	Depression deeper and not confined to posterior edge (either more centrally located or running proximo-anteriorly). Posterior contour more abruptly angular with point of greatest depth 5 to 8 mm. below tip of calcaneum	Similar to <i>plancus</i> , but depression extending markedly proximally and anteriorly. Posterior contour similar to <i>plancus</i> , with point of greatest depth 8.3 mm. below tip of calcaneum	Depth and extent of depression similar to <i>lutosus</i> . Contour generally angular, but some tending to round. Point of greatest depth 7 to 11 mm. below tip of calcaneum

TARSOMETATARSUS (*continued*)

	<i>P. cheriway</i>	<i>P. planicus</i>	<i>P. lutosus</i>	<i>P. prelutosus</i>
Position of distal foramina on posterior side	Distal-most foramen above border of intertrochlear space. Distance between foramina varying from actual union of the two to separation of 2.8 mm.	Distal-most foramen slightly above intertrochlear border. Distance between foramina varying from 2.7 mm. to 3.4 mm.	Distal-most foramen on border of intertrochlear space, opening distally. Distance between foramina 4.6 mm.	117 out of 238 bones have distal-most foramen at border of intertrochlear space as in <i>lutosus</i> . Others varying from slightly above the border to within 2.0 mm. of upper foramen. Greatest separation of the two foramina, 5.8 mm.
Greatest length: skins	81.0-95.9 mm. (89.7 mm. mean)	88.8-107.0 mm.* (96.3 mm. mean)	84.0-95.1 mm. (90.6 mm. mean)	
skeletons	87.8-97.1 mm. (94.3 mm. mean)	88.3-101.7 mm. (92.3 mm. mean)	92.2 mm.	81.9-94.8 mm. (88.6 mm. mean)
Breadth of proximal end	13.0-13.7 mm.	13.6-15.1 mm.	13.8 mm.	12.1-14.0 mm.
Breadth of distal end	14.4-15.5 mm.	14.9-16.7 mm.	14.6 mm.	13.0-15.5 mm.
Breadth of shaft at middle	5.2-5.7 mm.	5.4-6.6 mm.	5.7 mm.	4.8-6.0 mm.
Breadth of middle trochlea	4.8-5.3 mm.	5.3-6.0 mm.	5.2 mm.	4.4-5.5 mm.
Ratio of breadth of proximal end to length	13.7-14.9 per cent (14.1 per cent mean)	14.8-15.9 per cent (15.3 per cent mean)	14.9 per cent	13.4-16.1 per cent (14.7 per cent mean)
Ratio of breadth of distal end to length	15.1-16.7 per cent (15.6 per cent mean)	16.4-17.8 per cent (17.0 per cent mean)	15.8 per cent	14.4-17.4 per cent (16.2 per cent mean)
Ratio of breadth of shaft to length	5.6-6.2 per cent (5.8 per cent mean)	5.6-7.4 per cent (6.5 per cent mean)	6.1 per cent	5.3-7.1 per cent (6.1 per cent mean)
Ratio of breadth of trochlea to length	5.2-5.6 per cent	5.9-6.4 per cent	5.6 per cent	4.9-6.0 per cent (5.6 per cent mean)

* Measurement of 4.7 inches (=119.4 mm.) given in Ridgway's Manual (1915, p. 254) must be a typographical error, intended for 4.2 inches as previously listed in his earlier work (1875, p. 455).

FOSSIL POLYBORI FROM OTHER LOCALITIES

Having determined that the Pleistocene caracara of Rancho La Brea is a distinct species, separable from *Polyborus cheriway* in many characters, it has seemed advisable to review the other occurrences of fossil caracara now recorded as *Polyborus cheriway*.

The localities (other than Rancho La Brea) from which *Polyborus cheriway* has previously been recorded include: McKittrick and Carpinteria (Pleistocene), California (L. H. Miller, 1922, p. 123; 1927, p. 156); Conkling Cavern and Shelter Cave (Quaternary), New Mexico (Howard and A. H. Miller, 1933, p. 16); and Seminole Field and Melbourne (Pleistocene), Florida (Wetmore, 1931, p. 31).

As might be anticipated, the bones from the nearby Pleistocene asphalt deposits of McKittrick and Carpinteria are assignable to the Rancho La Brea species, *prelutosus*.

The single tibiotarsus from Shelter Cave, unfortunately, is so fragmentary as to be of no diagnostic value in the light of the present studies. It should, therefore, be listed now as *Polyborus* sp.

Among the specimens from Conkling Cavern there is one carpometacarpus (L. A. Mus. No. 106) which shows the characteristic crest of the inner side of the trochlea, the excavated area just below this crest, and the marked excavation beneath the pisiform process which marks *prelutosus* as distinct from *cheriway*. A distal end of tarso-metatarsus (L. A. Mus. No. 107) has the distal foramina separated more widely than in *cheriway* (3.1 mm.); and the presence of the distal edge of the well-marked groove on the internal side also distinguishes it from *cheriway*. Both of these characters agree with *plancus* as well as with *prelutosus*. However, since they are found in connection with the carpometacarpus, definitely identifiable as *prelutosus*, I have no hesitation in so assigning the tarsus also. Other specimens of ulna and humerus from Conkling Cavern are too fragmentary for definite identification, though it is noteworthy that in previous attempts to identify these bones I had observed the fact that they did not seem to fit in with *cheriway*, especially in stoutness. This observation is, of course, in keeping with the variable species *prelutosus*.

Dr. Wetmore's cooperation in allowing me to examine the specimens from Florida enables me to record the species *prelutosus* from that locality also. Of the fourteen specimens available, at least six are definitely similar to *prelutosus*. These include four distal ends of tarsometatarsi and two distal ends of humeri. The tarsi are smaller than available specimens of *cheriway* (a fact noted by Wetmore also, *loc. cit.*) and agree in size with some individuals of *prelutosus* (breadth of distal end 13.2 to 13.7 mm., breadth of shaft 5.1 to 5.4 mm.). The distance between the distal foramina varies from 3.0 to 4.0 mm., thus

exceeding *cheriway*, overlapping *plancus*, and falling entirely within the range of *prelutosus*. One specimen shows the distal tip of the groove of the internal side in a well-developed state, as in *prelutosus*. In the humeri, the tips of the ectepicondylar prominences are broken, but there is no suggestion of the heaviness and roundedness characteristic of *cheriway*. The area distal to the prominence on the palmar side is slightly raised as in *prelutosus*. The nearly complete specimen of ulna from Melbourne cannot be measured for exact length, but appears to equal the maximums of both *cheriway* and *prelutosus*. The breadth of distal trochlea also agrees with both species. The breadth of shaft, however, though within the range of *prelutosus*, is slightly greater than in *cheriway*.

Owing to overlapping characters in *prelutosus* and *cheriway*, the remaining fragmentary specimens from Florida (ulnæ, tibiotarsi, and femur) cannot be definitely identified as to species.

According to the above survey of fossil polybori, there remain no definite fossil records of *Polyborus cheriway*, and the geographic range of *Polyborus prelutosus* is extended to include New Mexico and Florida as well as California.

A comparison of the geologic and geographic ranges of the various species of *Polyborus*, as now indicated, follows:

<i>P. prelutosus</i>	Pleistocene	Southern U. S. from California to Florida
<i>P. latebrosus</i>	Prehistoric Recent	Puerto Rico
<i>P. lutosus</i>	Recent (extinct)	Guadalupe Island
<i>P. plancus</i>	Pleistocene to Recent	Brazil (Winge, 1888 ¹) South America from Amazon River to Peru, south to Straits of Magellan
<i>P. cheriway</i>	Recent	Southern U. S. from Arizona to Florida, south through Lower California, Cuba, Central America to northern South America

CONCLUSIONS

The determination of the proper allocation of the Rancho La Brea caracara with respect to the other known species of the genus *Polyborus* has presented an unusual problem and one which could not be solved by simple taxonomy. A review of the characters of *prelutosus*, as presented in the foregoing tables, shows the major trend of the species to be toward *plancus* and *lutosus*, and in the carpometacarpus, toward *latebrosus* as well. However, its range of variability extends so as to overlap *cheriway* also, and further includes some characters peculiar to itself alone. *Prelutosus* seems, therefore, to be a link be-

¹ See Lambrecht, 1933, pp. 729, 750.

tween the other known species. In fact, were it not for the time element involved, all the caracaras might be thought of as purely sub-specific divisions of one form.

Since our present system of classification would be utterly inadequate if all forms which have ever existed were available all together, it is clear that where a time hiatus exists, the species of the separate periods should be considered separately. The idea of possible sub-specific relationship between Pleistocene and Recent species seems to me to be wholly untenable. Undoubtedly *prelutosus* represents a form not far removed from, if not actually the ancestral type of, the Recent caracaras. Intergradation through such a species certainly cannot be evaluated in the same manner as intergradation of contemporaneous geographic races.

The relationship of the fossil to *lutosus*, which species it so closely approaches in size as well as in physical characters, is probably one of direct ancestry. Undoubtedly the once widespread *prelutosus* extended on to Guadalupe Island, either contemporaneously with its occurrence at Rancho La Brea, or, more probably, later as environmental changes on the continent were bringing about the gradual migration of individuals unable to keep pace with changing conditions. With suitable environment on the island, the portion of the species thus isolated could persist with only the slight modifications which are the usual result of continued inbreeding of a small sector of a variable species. In my opinion the differences noted between *prelutosus* and *lutosus* may be accounted for in this way, and are of sufficient importance to separate the two specifically. To call the ancestral, widespread *prelutosus* by the name of a single inbred, isolated remnant would be to overlook the various other ramifications of the species which overlap *plancus*, *cheriway*, and *latebrosus*.

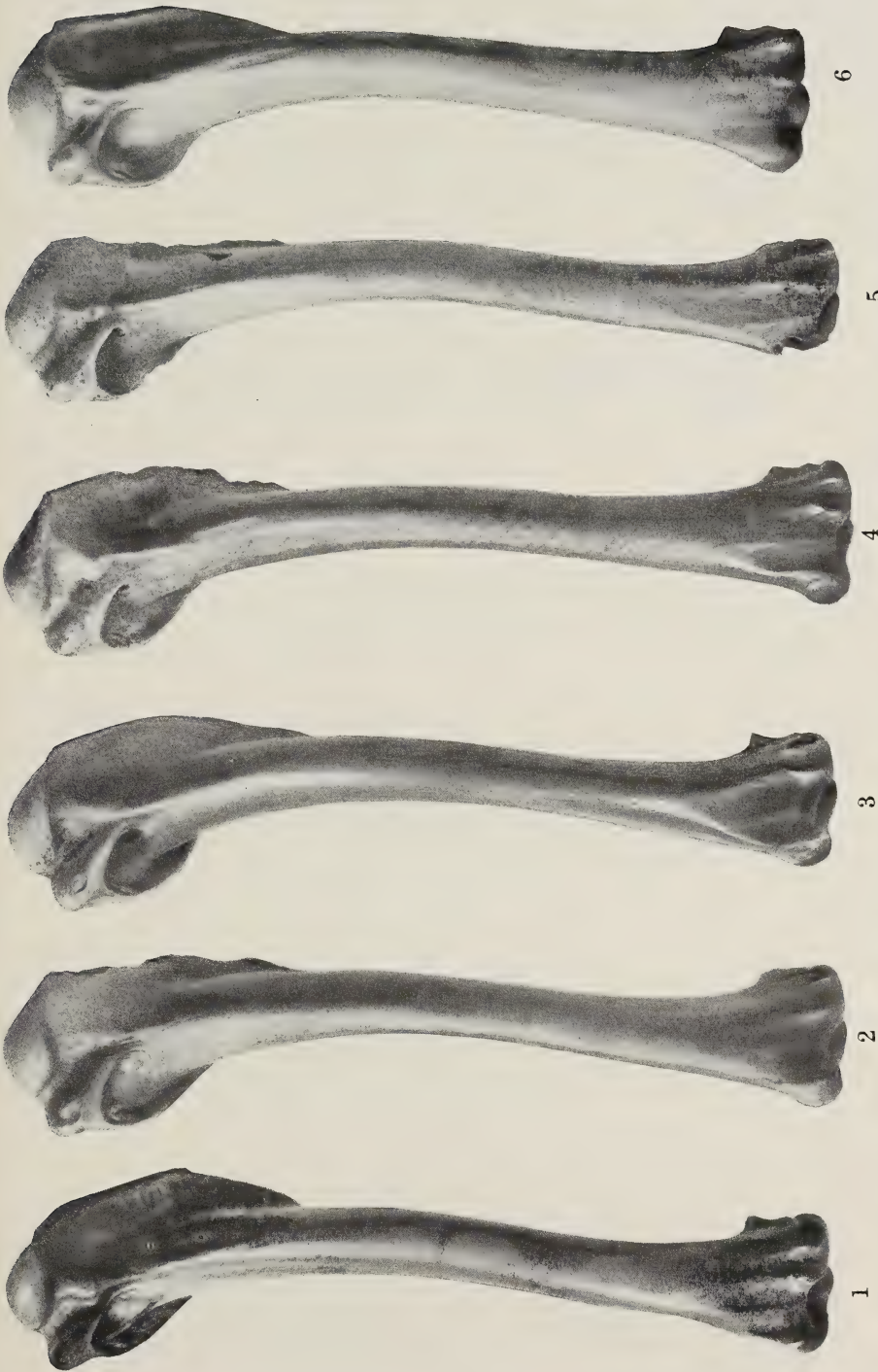
The situation accords well with Matthew's theory of dispersal of animals (1915, p. 180): "Whatever agencies may be assigned as the cause of evolution of a race, it should be at first most progressive at its point of original dispersal, and it will continue this progress at that point in response to whatever stimulus originally caused it and spread out in successive waves of migration, each wave a stage higher than the previous one. At any one time, therefore, the most advanced stages should be nearest the center of dispersal, the most conservative stages farthest from it." For, as he continues, "it is the environment itself, biotic as well as physical, that migrates, and the primitive species are those which have followed it, while those which remained have had to adapt themselves to a new environment and become altered thereby."

Considering Recent *Polyborus* in the light of this theory, we have, on the one hand, South American *plancus*, Guadalupe Island *lutosus*,

and Puerto Rican *latebrosus*. All these species more closely resemble Pleistocene *prelutosus* and each other than *cheriway*, and may therefore be considered as "primitive." All are remote from the Pleistocene habitat of *prelutosus* as revealed by the fossil records here reviewed. Remoteness is here taken in the sense defined by Matthew (*op. cit.*, p. 201) "not as a matter of geographical distance but of inaccessibility to invasion conditioned by the habitat and facilities for migration and dispersal." *Polyborus plancus* perhaps represents one of the earlier waves of migration, which, under particularly satisfactory conditions, has attained larger size. *Latebrosus* and *lutosus* may likely represent later, contemporaneous waves of migration, differing because of isolated inbreeding of slightly different combinations of parental characters. On the other hand we have *cheriway*, which by reason of its greater dissimilarity to *prelutosus* (as representing the ancestral type) may be considered the most advanced of all of the species. We find this "advanced" species inhabiting today some of the same territory occupied by *prelutosus* in the Pleistocene, thus of all Recent species being the nearest to the Pleistocene center of dispersal.

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Series of humeri of *Polyborus preclutusus*, with humerus of *Polyborus hotosus* for comparison, chosen to show range of variation in region of pneumatic fossa. Ulnar view, $\times 1$.
FIGS. 1-5—*P. preclutusus*: fig. 1, L. A. M. No. E4398 (type); fig. 2, L. A. M. No. E4356; fig. 3, L. A. M. No. E3927; fig. 4, L. A. M. No. E9852; fig. 5, L. A. M. No. E3255.
FIG. 6—*P. hotosus*, U. S. Nat. Mus. No. 19916.



Series of humeri of *Polyborus prelutosus*, with humerus of *Polyborus lutosus* for comparison, chosen to show range of variation in contour of bicipital crest. Palmar view, $\times 1$.
FIGS. 1-5—*P. prelutosus*: fig. 1, L. A. M. No. E3927; fig. 2, L. A. M. No. E1318; fig. 3, L. A. M. No. E4398 (type); fig. 4, L. A. M. No. E4356; fig. 5, L. A. M. No. E1804.
FIG. 6—*P. lutosus*, U. S. Nat. Mus. No. 19916.

PLATE 3

Bones of *Polyborus prelutosus* with corresponding elements of *Polyborus lutosus* and *Polyborus latebrosus* for comparison. $\times 1$.

FIG. 1—Rostrum of *P. lutosus*, U. S. Nat. Mus. No. 19916.

FIG. 2—Rostrum of *P. prelutosus*, L. A. M. No. E4485.

FIGS. 3, 3a—Internal and external views of carpometacarpus of *P. lutosus*, U. S. Nat. Mus. No. 19916.

FIGS. 4, 4a—Internal and external views of carpometacarpus of *P. prelutosus*, L. A. M. No. E3556.

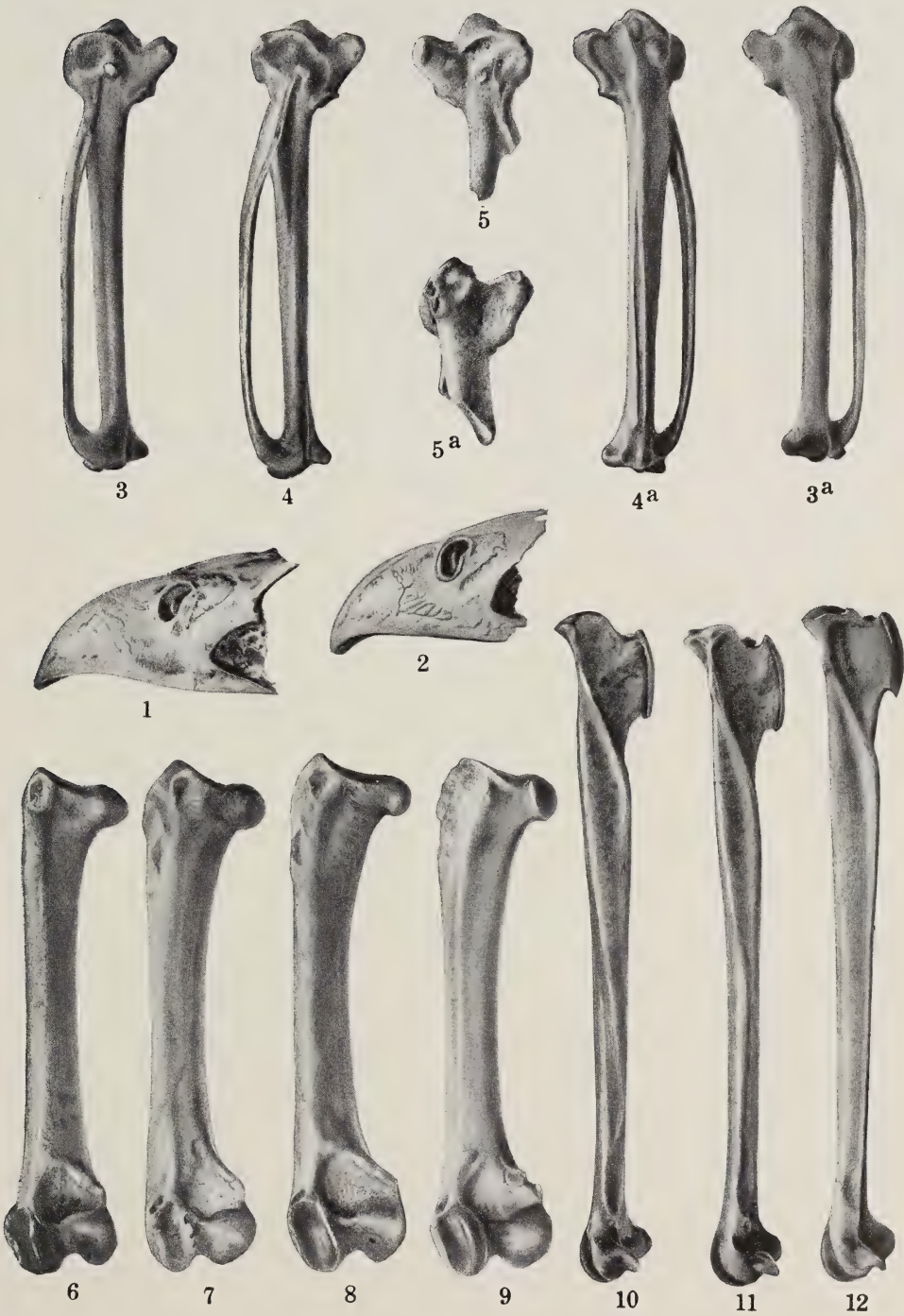
FIGS. 5, 5a—Internal and external views of carpometacarpus of *P. latebrosus* (type), Am. Mus. Nat. Hist. No. 4921.

FIGS. 6-8—Posterior view of femora of *P. prelutosus* chosen to show variation: fig. 6, L. A. M. No. E1210; fig. 7, L. A. M. No. E4012; fig. 8, L. A. M. No. E651.

FIG. 9—Posterior view of femur of *P. lutosus*, U. S. Nat. Mus. No. 19916.

FIGS. 10, 11—Internal view of tarsometatarsi of *P. prelutosus* showing variation in posterior contour of shaft near proximal end: fig. 10, L. A. M. No. E681; fig. 11, L. A. M. No. E3446.

FIG. 12—Internal view of tarsometatarsus of *P. lutosus*, U. S. Nat. Mus. No. 19916.



CONTRIBUTIONS TO PALÆONTOLOGY

VI

PLIOCENE PECCARIES FROM THE PACIFIC COAST
REGION OF NORTH AMERICA

By EDWIN H. COLBERT

With six plates and four text-figures

[Issued May 25, 1938]

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PLIOCENE PECCARIES FROM THE PACIFIC COAST REGION OF NORTH AMERICA

INTRODUCTION

During the past few years the California Institute of Technology has been fortunate in securing remains of upper Tertiary peccaries from various localities and horizons in the Pacific Coast region. These fossils were found in California, Nevada, and Oregon and for the most part they belong to the genus *Prosthennops*. A few of them, specifically the ones of upper Miocene age, have been described recently by Bode (1935), by Scharf (1935), and by Stock (1937). It is the purpose of this paper to describe the remaining specimens, comprising the bulk of the collection, all of which are of Pliocene age.

Some of this material is unusually abundant. The specimens from Kern River in California comprise a series of more than twenty upper and lower dentitions, all referable to a single species, thus affording for the first time an opportunity to study a species of the genus *Prosthennops* on the basis of a fairly adequate series of teeth, showing variations in size and in cusp patterns. This is a welcome addition to our knowledge of *Prosthennops*, for heretofore its several species have been founded on single specimens, on very few specimens of a fragmentary nature, or, as in the case of the Snake Creek discoveries, on numerous but disassociated single teeth.

Although the material from other Pliocene localities described in this paper is less abundant and not so well preserved as that from Kern River, it nevertheless offers valuable additional evidence as to the presence and the relationships of *Prosthennops* in the Pliocene of the Pacific Coast area.

I am happy to acknowledge my indebtedness to Dr. Chester Stock, not only for opportunity to study the peccary materials in the collections of the California Institute of Technology, but also for help in supervising and furnishing the illustrations, supplying information concerning the occurrence of Pliocene peccaries, and giving suggestions in the text.

REVIEW OF THE PLIOCENE PECCARIES OF THE PACIFIC COAST REGION

SIESTAN FORMATION

Prosthennops sp.

J. C. Merriam, Vertebrate Fauna of the Orindan and Siestan Beds in Middle California. Univ. Calif. Publ., Bull. Dept. Geol., vol. 7, 378-380, fig. 5, 1913.

Material—U. C. No. 19826, a palate with cheek teeth.

Horizon and locality—Siestan beds, Pliocene; Bald Peak near Berkeley, California.

Remarks—The characteristic features of this specimen are its very broad cheek teeth, the large P₂ and the molariform P₄.

CHANAC FORMATION

Prosthennops sp.

J. C. Merriam, Mammalian Remains from the Chanac Formation of the Tejon Hills, California. Univ. Calif. Publ., Bull. Dept. Geol., vol. 10, 126-127, 1916.

Material—U. C. No. 22459, "a number of fragments."

Horizon and locality—Chanac formation, Pliocene; Tejon Hills, California.

Remarks—Fragmentary material referred by Merriam to *Prosthennops*.

RATTLESNAKE FORMATION

Prosthennops oregonensis, n. sp.

(See page 255)

Prosthennops sp.

J. C. Merriam, Chester Stock, and C. L. Moody, The Pliocene Rattlesnake Formation and Fauna of Eastern Oregon; with Notes on the Geology of the Rattlesnake and Mascall Deposits. Carnegie Inst. Wash. Pub. No. 347, 83-86, figs. 37-40, 1925.

Material—U. C. Nos. 23862, a right maxilla; 22861, a mandibular symphysis; 23863, 23864, fragments of mandibular rami; 23865, a cuboid.

Horizon and locality—Rattlesnake formation, Pliocene; John Day River, Oregon.

Remarks—The specimens described by Merriam, Stock, and Moody are here referred to the new species *Prosthennops oregonensis*, described below. See p. 255.

KERN RIVER FORMATION

Prosthennops kernensis, n. sp.

(See page 248)

THOUSAND CREEK FORMATION

Prosthennops sp.

(See page 259)

Prosthennops sp.

J. C. Merriam, Tertiary Mammal Beds of Virgin Valley and Thousand Creek in Northwestern Nevada. Part II: Vertebrate Faunas. Univ. Calif. Publ., Bull. Dept. Geol., vol. 6, 272-276, figs. 52, 53, 54, 1911.

Material—U. C. No. 11876, an inferior canine, a left upper second and third premolar, an upper third molar; No. 11884, an upper third premolar; No. 19416, a mandibular symphysis.

Horizon and locality—Thousand Creek beds, Pliocene; Thousand Creek, Nevada.

Remarks—These specimens are too fragmentary for specific identification. They are possibly specifically identical with the new material from Thousand Creek, described below (p. 259). It might be pointed out that the material described by Merriam is characterized by a rather triangular second upper premolar, a well-developed cingulum on the posterior portion of the third upper premolar, and a strong talonid on the third upper molar. There are no intermediate conules in the valley of this last tooth.

J. C. Merriam and Chester Stock, A Further Contribution to the Mammalian Fauna of the Thousand Creek Pliocene, Northwestern Nevada. Carnegie Inst. Wash. Pub. No. 393, 19-20, fig. 12, 1928.

Material—U. C. No. 30040, right P₂₋₃ and left P₄.

Horizon and locality—Thousand Creek beds, Pliocene; Loc. 2744, U. C. Mus. Paleontology, northwestern Nevada.

Remarks—This specimen, quite definitely referable to the genus *Prosthennops*, is characterized by its large, tricuspid P₂ and its large size. It is possibly specifically identical with the material described below (p. 259). More detailed comparisons will be found in the description cited above.

MOUNT EDEN FORMATION

Prosthennops edensis Frick

Childs Frick, Extinct Vertebrate Faunas of the Badlands of Bautista Creek and San Timoteo Canyon, Southern California. Univ. Calif. Publ., Bull. Dept. Geol., vol. 12, 350-354, figs. 58-63, 1921.

Type—U. C. No. 23369, a maxilla with P₃-M₂.

Referred—U. C. Nos. 23370, a fragmentary mandibular ramus with P₃-M₃; 23775, a portion of M₃; 23776, a premolar; 23777, an upper molar; 23778, an incisor.

Horizon and locality—Mount Eden formation, Pliocene; Univ. Calif. Loc. 3269, near Mount Eden, in the vicinity of Beaumont, California.

Remarks—This is a rather large species of *Prosthennops*, characterized by its low-crowned cheek teeth and by the relatively small size of the third premolar.

Platygonus sp.

Childs Frick, Extinct Vertebrate Faunas of the Badlands of Bautista Creek and San Timoteo Canyon, Southern California. Univ. Calif. Publ., Bull. Dept. Geol., vol. 12, 354-356, figs. 64, 65, 1921.

Material—U. C. Nos. 23439, 23440, canine teeth.

Horizon and locality—Mount Eden formation, Pliocene; San Timoteo Canyon, California.

Remarks—These specimens were referred to *Platygonus* because of their large size.

ROME FORMATION

Prosthennops serus (?) (Cope)

(See page 257)

ETCHEGOIN FORMATION

Platygonus sp.

J. C. Merriam, Tertiary Vertebrate Faunas of the North Coalinga Region of California. Trans. Amer. Philos. Soc., (2), vol. 22, 32, fig. 32, 1915.

Material—U. C. No. 21371, an astragalus.

Horizon and locality—Etchegoin, *Pliohippus coalingensis* zone, Pliocene; North Coalinga region, California.

Remarks—This specimen might be referable either to *Prosthennops* or to *Platygonus*.

Mylohyus-like form

J. C. Merriam, Tertiary Vertebrate Faunas of the North Coalinga Region of California. Trans. Amer. Philos. Soc., (2), vol. 22, 37, figs. 40, 41, 1915.

Material—U. C. Nos. 21359, 21360, two lower third molars; No. 21338, a phalanx.

Horizon and locality—Upper Etchegoin, upper Pliocene or Pleistocene; North Coalinga region, California.

Remarks—The lower molars were compared by Merriam with *Platygonus*, *Mylohyus*, and *Tayassu*. From the illustrations it would seem possible that they are referable to *Prosthennops*, for they show certain similarities to the rather large and robust Eden species, *Prosthennops edensis*.

COSO FORMATION

Platygonus sp.

(See page 261)

J. R. Schultz, A Late Cenozoic Vertebrate Fauna from the Coso Mountains, Inyo County, California. Carnegie Inst. Wash. Pub. No. 487, 101–102, pl. 8, figs. 3–6, 1937.

PLIOCENE, EXACT LEVEL NOT DETERMINED

Tayassu hesperius (Marsh)

O. C. Marsh, Notice of Some New Fossil Mammals from the Tertiary Formation. Amer. Jour. Sci., (3), vol. 2, 42–43, 1871. (*Dicotyles hesperius*.)

Type—Portion of a right jaw.

Horizon and locality—"Pliocene," Oregon.

***Prosthennops* (?) *condoni* (Marsh)**

O. C. Marsh, Notice of Some New Fossil Mammals from the Tertiary Formation. Amer. Jour. Sci., (3), vol. 2, 41, 1871. (*Platygonus condoni*.)

Type—Yale Peabody Museum, No. 11869, portion of a right mandibular ramus with M1-3.

Horizon and locality—Mascall formation (?), middle Miocene according to Matthew, Pliocene according to Thorpe.

***Prosthennops* (?) *rex* (Marsh)**

O. C. Marsh, Description of Tertiary Artiodactyles. Amer. Jour. Sci., (3), vol. 48, 273-274, figs. 31, 32, 1894. (*Platygonus rex*.)

Type—Yale Peabody Museum, No. 11870, molar teeth.

Horizon and locality—Rattlesnake formation (?); Wilsons Springs, Crooked River, Oregon.

Remarks—Little can be said about the foregoing three forms, for they are based on very poor material, the exact geologic positions of which are not known. Thorpe (1924) has referred *Platygonus condoni* and *Platygonus rex* to the genus *Prosthennops*.

***Prosthennops longirostris* Thorpe**

M. R. Thorpe, A New Species of Extinct Peccary from Oregon. Amer. Jour. Sci., (5), vol. 7, 393-397, figs. 1-4, 1924.

Type—Yale Peabody Museum, No. 11160, a mandible with the dentition well preserved; also fragments of an associated skull, including a portion of the left maxilla with M1-3.

Horizon and locality—Pliocene; "near the John Day Region, Oregon."

Remarks—*Prosthennops longirostris* is a distinctive form of large size, characterized by unusual length of the diastema between the canines and the premolars. It is particularly unfortunate that the geologic position of this species is unknown. There seems to be little doubt, however, that it is of Pliocene age.

STRATIGRAPHIC OCCURRENCE AND AGE

The peccary remains described in this paper come from five stratigraphic horizons, indicated as follows:

Coso formation, Coso Mountains, Inyo County, Calif.: *Platygonus* sp.

Rome deposits, Owyhee River, Malheur County, Ore.: *Prosthennops serus* (?) (Cope)

Thousand Creek formation, northwestern Nevada: *Prosthennops* sp.

Rattlesnake formation, John Day basin, Oregon: *Prosthennops oregonensis*, n. sp.

Kern River formation, Kern County, Calif.: *Prosthennops kernensis*, n. sp.

With the exception of the Coso formation, all the stratigraphic horizons listed above are currently regarded as of middle Pliocene age. Among these the Rome and Thousand Creek deposits are presumably closely related in time, as shown by resemblances in their faunas. Resemblance to these assemblages is seen likewise in the fauna from the Rattlesnake. Although the final report on the Kern River deposits and fauna has not been published, a suggestion is made¹ that the Kern River is more closely related to the several middle Pliocene horizons listed above than to the lower Pliocene Chanac and Ricardo of the Californian area. The Coso is definitely a later horizon, and its age determination as late Pliocene or early Pleistocene has been discussed recently by Schultz.²

DESCRIPTION OF NEW MATERIAL

Prosthennops kernensis, n. sp.

Type—Calif. Inst. Tech. Coll. Vert. Pale., No. 224, a palate with the cheek teeth complete on both sides.

Paratypes—Calif. Inst. Tech. Coll. Vert. Pale., Nos. 225, a left mandibular ramus with DM3-4, M1; 226, a left mandibular ramus with M1-3; 227, a left mandibular ramus with P2-M3; 228, a left mandibular ramus with P3-4, M1, and part of M2; 229, symphysis of a mandible with the incisors and the right canine; 230, calcaneum and astragalus; 231, left mandibular ramus with P2-M2 and a part of M3; 233, fragment of a palate with right P2-M2; 234, left metatarsal IV; 236, portion of right ramus with P4, M1-2; 237, left metacarpal III; 239, portion of left premaxilla and maxilla with canine; 240, fragment of right ramus with P3-4; 240A, right M3; 241, right mandibular ramus with P2-M3; 545, fragment of left maxilla with P3-M3, also P3 and M3 of the left side, probably belonging to the same individual; 547, fragment of mandibular ramus with right P2-3; 548, mandibular symphysis with the left canine and the base of the right canine; 551, fragment of right ramus with P3-4; 553, part of left maxilla with P2-4 and alveolus of canine, also a right M3; 1937, right ramus with DM3-4; 1938, portion of right ramus with DM2-4; 1939, part of left ramus with DM4; 2038, right ramus with deciduous incisors, canine, and DM2-4; 2141, right M3; 2142, P2.

Referred specimen—Calif. Inst. Tech. Coll. Vert. Pale., No. 1940, crushed symphysis with incisors and canines, also right P3.

Horizon—Kern River formation, middle Pliocene.

Locality—Calif. Inst. Tech. Vert. Pale. Loc. 49 and 50, Kern River beds, approximately 9 miles northeast of Bakersfield, California.

Diagnosis—A *Prosthennops* of medium size, closely comparable in this respect to *Prosthennops crassigenis* and *Prosthennops niobrarensis*. Upper premolars relatively large, their combined length being greater than the length of the first two molars and approximately equal to the length of the

¹ Chester Stock, oral communication.

² J. R. Schultz, Carnegie Inst. Wash. Pub. No. 487, 86-98, 1937.

last two molars. The second upper premolar is large and has a quadrate outline, whereas in other species this tooth tends to be trihedral in outline. The third upper premolar approaches a molariform state and the fourth upper premolar is completely molariform. Upper molars rather broad, but without cingula; the third upper molar is characterized by the narrowness of its posterior portion.

There are constantly only two lower incisors on either side, a feature in which this species resembles *Prosthennops longirostris*. Incisors of relatively large size. Lower canines large, with triangular cross section. Lower premolars relatively large, as is the case with the upper premolars. Fourth lower premolar almost entirely molariform; third lower premolar less molariform, but approaching the structure of the tooth behind it. Lower molars rather broad and robust and seemingly somewhat more hypsodont than in most species of *Prosthennops*; third lower molar with wide talonid.

Comparisons—The diagnosis presented above outlines the salient characters of this new species of *Prosthennops*. It may be advantageous, however, to discuss in some detail the various specimens on which the species is founded, thereby presenting additional information concerning the dental characters of this new form and indicating the extent to which individual differences are apparent as shown by the material at hand.

The type palate, No. 224, is perhaps the best specimen in the collection, since the premolars and molars are perfectly preserved on both sides. This specimen shows all the diagnostic characters of the species, namely the relatively large premolars, the quadrate second premolar, the broad molars without cingula, and the narrowness of the posterior portion of the third molar. Two other maxillary fragments, Nos. 233 and 553, show the premolars to advantage, and in both of these specimens (as in the type) the second and third premolars are large and well advanced toward acquisition of the molariform pattern, while the second premolar is relatively large, with a quadrate outline. Evidently these are constant characters in *Prosthennops kernensis*. In the generic type, *Prosthennops crassigenis*, the cheek teeth are very much worn, so that it is impossible to make any really definite statements about their structure, but it would appear that the premolars are definitely smaller than these teeth in the California species, while the third premolar of the generic type seems less molariform than the corresponding tooth in *Prosthennops kernensis*. In the referred skull of *Prosthennops serus* the premolars are considerably smaller than in the California species, and the second premolar is rather small and triangular in outline. In *Prosthennops niobrarensis* the last two premolars, while highly molariform, are relatively narrower than the comparable teeth in *Prosthennops kernensis* (*Prosthennops niobrarensis* is characterized by its narrow cheek teeth) and the second premolar has a triangular outline.

One of the above-mentioned maxillary fragments, No. 553, includes the left premolars and the alveolus of the canine. This specimen seems to show that the post-canine diastema in *Prosthennops kernensis* is slightly shorter than the hiatus in the tooth row of other species of the genus, for this diastema appears to be approximately equal to the combined length of the premolars, whereas in other species of *Prosthennops* it is longer than

the combined premolar length. Of course, the shorter diastema in *Prosthennops kernensis* may be attributed to the relatively large premolars in this species; that is, the enlargement of the premolars has caused them to encroach forward in the maxilla toward the canine. Another fragment of upper jaw, No. 239, contains a left canine, a rather small and laterally compressed tooth quite similar in size and shape to the canine of *Prosthennops crassigenis*. In this specimen the notch in the maxilla for the reception of the lower canine is broad and shallow.

The upper molars are intermediate between the very broad upper molars of the type of *Prosthennops crassigenis* and the referred skull of *Prosthennops serus*, and the relatively narrow molars of *Prosthennops niobrarensis*. These teeth in the species under consideration lack external cingula, in which respect they are decidedly different from the upper molars of the latter two of the above-mentioned forms, namely *Prosthennops serus* and *Prosthennops niobrarensis*. The third upper molar in *Prosthennops kernensis* is very narrow in its posterior portion, in which respect it resembles the comparable tooth of *Prosthennops* sp. from the Thousand Creek formation, described and figured by Merriam in 1911. A third superior molar, No. 545, supplements the type specimen and shows again the narrowness of the posterior portion of this tooth.

A considerable amount of variation in size is shown by the series of lower dentitions. The question of size variation in *Prosthennops kernensis* will be discussed at length in subsequent paragraphs of this paper; suffice it to say here that the largest of the lower jaws, No. 226, approaches the type mandible of *Prosthennops serus* in size and robustness of the molars, while the smallest one, No. 227, is perhaps 12 per cent smaller linearly than the first-mentioned specimen.

Three mandibular symphyses are preserved, Nos. 229, 548, and 1940. The first and third of these specimens are of medium size and are approximately equal to each other in their dimensions, but the second specimen, No. 548, is considerably larger than the other two, not only by reason of the robustness of its symphysis, but also because of its very large, heavy canines. A comparative study of these three specimens would indicate that the third lower incisor is on the point of disappearing in *Prosthennops kernensis*. It may be either present or absent, but when it is present it is very small and rudimentary. In No. 229 there are indications of an alveolus for the third incisor on the left side of the symphysis, but on the right side this tooth would seem to be absent. In No. 548 the incisors are not preserved, but the alveoli show that there was a third incisor on the right side but not on the left. In No. 1940 the third incisor is preserved on the right side as an extremely small tooth, and on the left side an alveolus may be seen.

No. 229 shows an interesting feature in the form of a lateral groove, worn into the external-lingual surface of the left middle incisor. This groove is broad, having an antero-posterior width of approximately 4.5 mm., and it cuts through the enamel into the dentine. Undoubtedly this groove was worn by the animal rooting in the ground, tearing up tough plant fibers with its teeth, and pulling upward on them with the lower incisors. Similar grooves are not uncommon in second lower incisors of modern peccaries, and they are often to be seen in the incisors of extinct entelodonts.

As was mentioned above, the canines of No. 548 are very large and heavy. A cross section of the right canine, which is broken off near the alveolus, shows this tooth to have a somewhat triangular outline, with a short posterior base and long internal and external sides. As a matter of fact, the internal face of the tooth is curved; the external face is also curved and in addition possesses a strong ridge; and the posterior face, where it is not worn, is indented by a deep central groove. The canines of the other two symphyses are similar to the tooth just described, but since they are much smaller, their external vertical ridges and posterior grooves are much less pronounced, thereby giving to their cross sections a more nearly triangular outline.

As might be expected, the lower premolars of *Prosthennops kernensis*, as seen best in Nos. 227 and 228, are relatively large, and the last two of these teeth have progressed toward a molariform structure. The fourth lower premolar is fully as large as the first molar, and it is made up of two pairs of transversely placed cusps. The third premolar is a small replica of the tooth which follows it. However, it may be noted that in both of these teeth the anterior cusps are much higher than the posterior cusps, in which respect these premolars show their true heritage, since they have not attained the molariform status of having anterior and posterior cusps equally developed. The second premolar is a small tooth, consisting of a central cone bordered in front by a basal cingular swelling, and having a broad posterior heel.

By following the premolars back, from the second to the fourth of the series, a graphic illustration of the manner in which these teeth assume a molariform structure may be obtained. This may best be seen in No. 231. As was pointed out above, the second premolar consists of an anterior cone and a posterior heel. It might be added that this posterior heel appears to be formed by a small cusp, developed medially just behind the central cone, on either side of which are cingular upgrowths. In the third and fourth premolars may be seen progressively the separation of the two anterior transversely placed cusps, by means of the development of a median longitudinal sulcus, and the upgrowth of the lateral cingular buds of the heel to form a pair of transversely placed posterior cusps. It would seem as if the original median cusp that was directly behind the main central cone were united with the external cingular bud, to form the postero-external cusp. In the more primitive teeth of *Prosthennops xiphodonticus* the third premolar is not molariform, but rather is a replica of the second premolar.

The lower molars need no elaborate description. They are very much like the upper molars, but are narrower and seemingly rather hypsodont. The third lower molar has a broad heel.

Five fragments of mandibular rami in the Kern River material contain milk molars. These are Nos. 225 with left DM3-4, M1; 1937 with right DM3-4; 1938 with right DM2-4; 1939 with right DM4; and 2038 with deciduous incisors, canine, and DM2-4. The fourth lower deciduous molar, as is typical of the artiodactyls, is elongated and consists of three pairs of transversely placed cusps. Quite an appreciable amount of size variation is shown in this tooth; for instance, the DM4 of 225 is noticeably longer

Measurements (in millimeters) of *Prosthennops kernensis*

Specimen No.	P2		P3		P4		M1		M2		M3	
	L.	W.	L.	W.	L.	W.	L.	W.	L.	W.	L.	W.
224.....	10.0	9.0	11.0	11.0	12.5	12.5	13.0	13.5	16.5	15.0	19.0	14.5
233.....	9.5	10.0	11.5	12.0	12.5	13.5	13.0	14.5	17.0	16.5
553.....	10.5	10.0	11.5	12.0	13.0	13.5
545.....	12.0	12.0	13.0	13.5	15.0	13.5	17.5	14.0	21.0	14.5

Specimen No.	P2		P3		P4		M1		M2		M3	
	L.	W.	L.	W.	L.	W.	L.	W.	L.	W.	L.	W.
226.....	16.0	13.0	17.5	14.0	24.0	14.5
227.....	9.5	6.0	11.0	8.0	13.0	10.0	12.5	11.0	15.5	12.5	22.0	13.0
228.....	11.5	9.5	15.0	12.5	15.5	12.5
231.....	10.5	7.5	11.5	9.5	14.0	11.5	14.0	11.5	16.5	13.0	...	13.5
236.....	15.0	12.0	14.5	11.5	18.0	14.5
240.....	13.0	10.0	14.5	11.0
240A.....	23.5	15.0
241.....	10.0	7.0	11.5	9.0	13.5	11.5	13.0	12.0	16.0	14.0	23.0	14.0
547.....	10.0	7.0	11.5	10.0
551.....	12.0	8.0	14.5	11.0

Specimen No.	DM2		DM3		DM4		MI		Medial DĪ: W.	Lateral DĪ: W.	DĪ: L.
	L.	W.	L.	W.	L.	W.	L.	W.			
225.....	11.5	7.0	19.0	11.0	16.0	12.0
1937.....	11.5	7.0	18.0	10.0
1938.....	9.5	5.5	11.5	7.5	20.5	10.0
1939.....	17.5	9.5
2038.....	11.8	6.7	18.9	8.5	3.4	3.0	3.8

Specimen No.	Width of palate at M1	Length of sym- physis	Width of sym- physis	II		I2		I3		Ĉ		
				L.	W.	L.	W.	L.	W.	L.	W.	H.
224.....	24.0
229.....	76.0	28.0	7.0	5.5	7.0	5.5	13.0	10.0	38.0
239*.....	14.0	8.0	29.0
548.....	81.0	31.0	16.0	12.0	48.0
1940.....	5.5	4.5	6.0	5.0	2.5	3.0	13.0	8.5	...

* Upper canine.

and very much heavier and more robust than the corresponding tooth in 1939. DM $\bar{2}$ is essentially a replica of P $\bar{2}$, while DM $\bar{3}$ is similar to P $\bar{3}$ but smaller. To explain more fully, DM $\bar{3}$ consists of two high transversely placed cusps, in front of which are two very small, low transversely placed cusps, and behind which is a broad, sloping heel. Numerous subsidiary rugosities of the enamel in addition to the principal cusps are present on the posterior milk cheek teeth. The two incisors in No. 2038 are of subequal size and in each the postero-dorsal face of the crown is slightly concave. The milk canine possesses a long, slender crown, slightly recurved with posterior edge rather well defined.

Skeletal remains of the Kern River peccaries are relatively rare in the collection. Two metapodials and an articulated calcaneum and astragalus

Ratios and indices, Prosthennops kernensis

Specimen No.	Length, P series (mm.)	Length, M series (mm.)	Ratio $\frac{P \text{ ser.} \times 100}{M \text{ ser.}}$	Indices					
				P $\bar{2}$	P $\bar{3}$	P $\bar{4}$	M $\bar{1}$	M $\bar{2}$	M $\bar{3}$
224	34.0	49.0	70	90	100	100	104	91	76
233	33.5	105	104	108	111	97	...
553	36.0	95	104	104
545	53.5	100	104	90	80	69
				P $\bar{2}$	P $\bar{3}$	P $\bar{4}$	M $\bar{1}$	M $\bar{2}$	M $\bar{3}$
226	58.0	81	80	60
227	34.0	51.0	67	63	73	77	88	80	59
228	82	83	81
231	37.0	71	83	82	82	79	...
236	80	79	80	...
240	77	76
240A	64
241	35.0	52.0	67	70	86	85	93	88	61
547	70	87
551	67	76

are shown in plate 1. One of the metapodials, metatarsal IV, No. 234 (plate 1, figure 4), is considerably smaller than the comparable bone, A. M. No. 14053, of *Prosthennops crassigenis* or *Prosthennops serus* from the Snake Creek formation. The Kern River metatarsal is approximately equal in length to the upper cheek teeth of the type specimen; in the modern *Tayassu* the metatarsals are considerably shorter than the upper cheek teeth. It is evident from this specimen that the metatarsals were entirely separated in *Prosthennops kernensis*, a character that would seem to be typical of the genus. Measurements (in millimeters) of No. 234 are: length, 83; width at mid-shaft, 9.5.

Variation in Prosthennops kernensis—A careful comparative study of the several dentitions of *Prosthennops kernensis* appears to show that except for size, there is surprisingly little variability within the species. The size variations are illustrated graphically in figures 1 and 2.

In the two symphyses, Nos. 229 and 548, the relative size of the third incisors seems to be about the same. The canines are markedly different

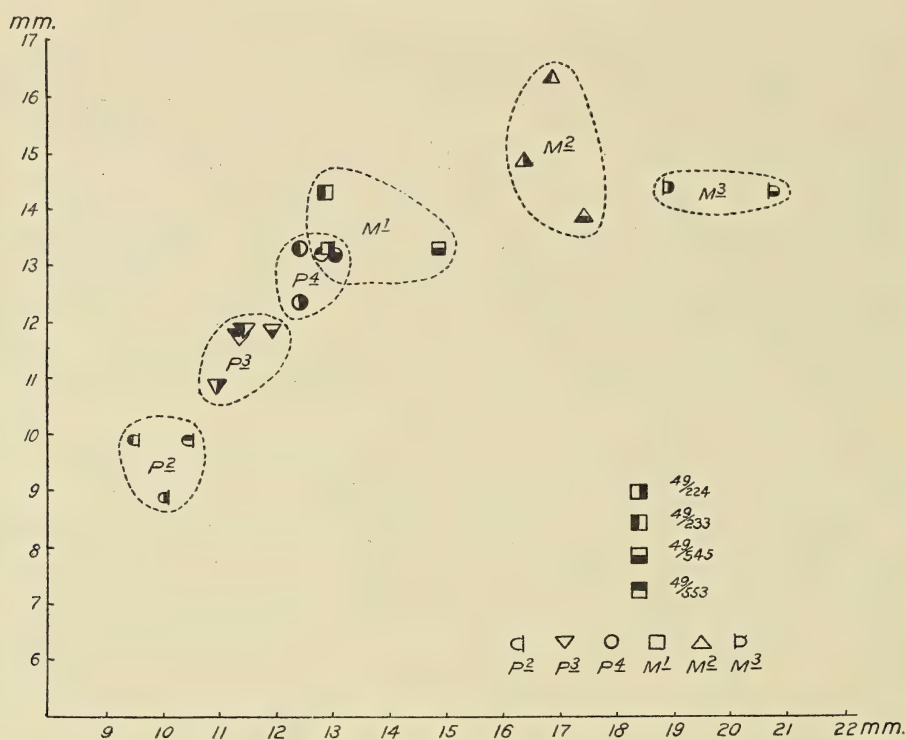


FIG. 1—Graph to show the variation in the upper cheek teeth of *Prosthennops kernensis*. Lengths on horizontal axis, widths on vertical axis.

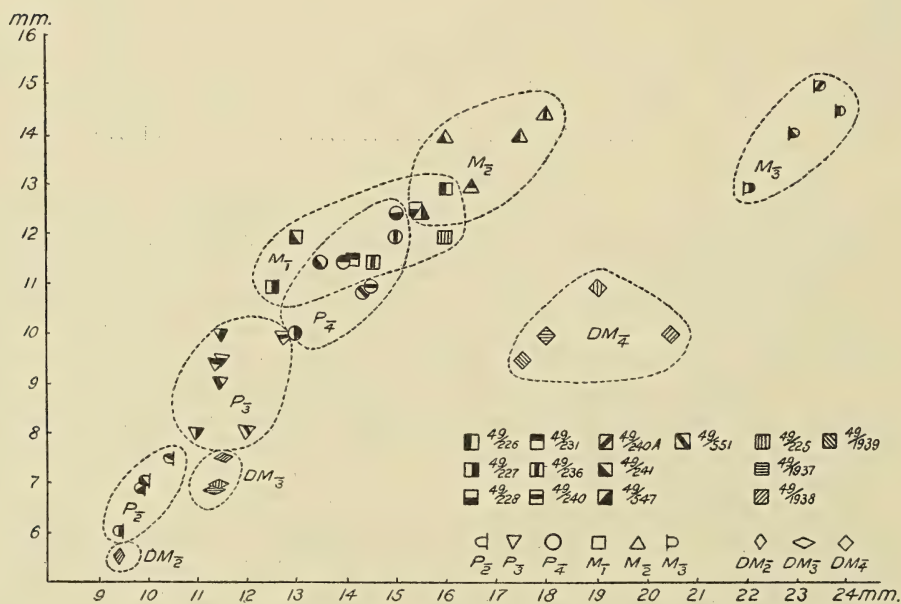


FIG. 2—Graph to show the variation in the lower cheek teeth of *Prosthennops kernensis*. Lengths on horizontal axis, widths on vertical axis.

in size in these two specimens, but this variation is undoubtedly due to sexual dimorphism rather than to true individual variation. In the upper dentitions the premolars are uniformly molariform, the relative breadth of the molars is about the same, the lack of cingula on the molars is characteristic of all the specimens, and the narrow posterior portion of the third molar is characteristic. Only one tooth, the second premolar, shows any appreciable amount of individual variation. This tooth, naturally more unstable than the rest of the cheek teeth, varies slightly in relative size and shape in the three specimens in which it is preserved. In the lower cheek teeth the second premolars are uniformly developed, as is the molarization of the last premolar; the breadth of the molars is rather uniform, the lack of cingula in these teeth is characteristic, and the development of the talonid is strikingly alike in all the specimens.

Therefore it would seem that these characters are rather constant within the species, and that the principal individual variation as shown in the teeth occurs in the character of size.

***Prosthennops oregonensis*, n. sp.**

Type—Calif. Inst. Tech. Coll. Vert. Pale., No. 535, a palate with cheek teeth complete on both sides, both canines and left incisors.

Paratype—Calif. Inst. Tech. Coll. Vert. Pale., No. 533, a palate of a very old individual, with the cheek teeth on both sides.

Horizon—Rattlesnake formation, middle Pliocene.

Locality—Calif. Inst. Tech. Vert. Pale. Loc. 21, Rattlesnake beds, north of Rattlesnake Creek and west of saddle between the two rhyolite-capped buttes of type section. Reddish-colored old soils forming part of westerly continuation of Rattlesnake beds at type section. John Day Valley, Oregon.

Diagnosis—A *Prosthennops* of average size, being comparable in this respect with the generic type, with *Prosthennops niobrarensis*, and with *Prosthennops kernensis*. The upper premolars are relatively large, as in the latter two species cited above, their combined length being greater than the length of the first two molars and approximately equal to the length of the last two molars. The second upper premolar is large, but its outline is triangular, rather than quadrate as is the case in *Prosthennops kernensis*. The fourth upper premolar is molariform, and the third premolar approaches the molariform pattern. Upper molars moderately broad and without internal cingula, this latter being a character distinguishing the new species from *Prosthennops longirostris*. Posterior half of third molar broad, as contrasted with the narrow posterior portion in the third molar of *Prosthennops kernensis*. Upper incisors large, the first incisor being especially robust. Canines transversely flattened. Notch for lower canine rather small, while the maxilla above the canine is not greatly expanded. Canine-premolar diastema of average length, being comparable with the diastema in *Prosthennops crassigenis* and *Prosthennops kernensis*, and considerably shorter than the diastema in *Prosthennops longirostris*.

Description and comparison—Most of the diagnostic characters of this new species must be obtained from the type palate, since the paratype

specimen is of a very old animal, with teeth so greatly worn that it shows very little in the way of dental structures. The characters of this new species have been rather fully outlined in the diagnosis, so there is little need for a lengthy description of the type and paratype specimens.

One of the striking features of the type palate is the large size of the incisors, especially of the first incisor. In this respect *Prosthennops oregonensis* is like *Prosthennops niobrarensis* and like the palate referred by Matthew to *Prosthennops serus*, and quite unlike *Prosthennops crassigenis*. It may be noted here that the first incisor in this new species is not only comparatively but also actually larger than the comparable tooth in any of the other species of *Prosthennops*. The second incisor of *Prosthennops oregonensis* is relatively quite small, as compared with the tooth in front of it. There is no third incisor—an absence frequently noted in *Prosthennops*. The canines are rather small and transversely flat, but this may be due in part to the fact that we are dealing here with a young animal in which the canines have only begun their protrusive growth.

The other tooth characters have been set forth in the diagnosis. Attention may be called here to the fact that the second premolar is large but of triangular outline and that the last molar is posteriorly broad with a wide heel. There are no internal cingula in the molars, but small external cingula may be seen, blocking the external openings of the transverse valleys. Of course there are well-developed anterior and posterior cingular shelves, as in other species of *Prosthennops*. Small accessory cusps are present in the median valleys; these show particularly well in the third molars.

The infraorbital foramen is visible on the left side of the type specimen. It is very large, and is located above the last two premolars.

The paratype specimen, although adding little to the diagnostic characters of the species, is particularly interesting because it demonstrates certain changes in the skull and dentition due to extreme old age. The teeth in this specimen are worn smooth, so that all traces of the cusps (except for the metacone of the last molars) have completely disappeared. The first molar on the right side dropped out during the life of the animal, and the alveolus was obliterated by a growth of bone. The original surface of the palate is covered by a secondary exostosis, a further proof of the very great age of this individual. This specimen shows particularly well the large size and deep excavation of the infraorbital foramen.

The question arises as to the relationships of this new species, *Prosthennops oregonensis*. *Prosthennops longirostris*, described by Thorpe in 1924, was found in eastern Oregon, "near the John Day Region," in beds reputedly of Pliocene age. Consequently there is a possibility that it came from the Rattlesnake formation. Certain characters indicate, however, that *Prosthennops longirostris* is definitely specifically distinct from the new species here described; its long muzzle (as inferred from the long premolar-canine diastema of the mandible) and the well-developed internal cingula of the molars set it apart from *Prosthennops oregonensis*.

But what are the relationships of this new species to the *Prosthennops* material from the Rattlesnake formation, described by Merriam, Stock, and Moody in 1925? Comparisons are difficult, because the maxilla, Univ.

Calif. Coll. No. 23862, contains, besides the deciduous teeth, only a first molar that may be compared directly with the teeth of *Prosthennops oregonensis*. This tooth is closely comparable in size and form with the corresponding tooth of the new species now being described. Moreover, there is nothing to preclude the lower jaw material described by Merriam, Stock, and Moody from belonging to the new species, *Prosthennops oregonensis*. Of course, the symphysis, Univ. Calif. Coll. No. 22861, is robust, with very large incisors and canines, but in view of the size variation in a single species of *Prosthennops*, as shown by the study of *Prosthennops kernensis*, this symphysis is well within the range of the expected variation in *Prosthennops oregonensis*. The large lower incisors, too, might indicate a real specific affinity with the large upper incisors of the new species described in this paper.

Consequently it seems logical to suppose that *Prosthennops* sp., described by Merriam, Stock, and Moody from the Rattlesnake formation, is referable to the species *Prosthennops oregonensis*.

Comparative measurements (in millimeters) of
Prosthennops oregonensis and *Prosthennops longirostris*

	<i>P. oregonensis</i>						<i>P. longirostris</i>		
	C. I. T. No. 535			C. I. T. No. 533			Y. P. M. No. 11160		
	L.	W.	Ind.	L.	W.	Ind.	L.	W.	Ind.
I1.....	12.0	8.5
I2.....	4.5	7.5
C.....	14.0	8.0
P2.....	11.0	9.5	86	10.5	9.5	80
P3.....	11.5	11.5	100	11.0	12.5	114
P4.....	12.5	12.0	96	12.5	12.5	100
M1.....	15.0	12.5	83	11.0	13.0	118	16.8
M2.....	17.0	14.0	82	16.5	15.0	91	19.2	17.1	89
M3.....	20.0	14.0	70	19.0	15.0	79	20.5	16.3	80
P series.....	37.0	34.0
M series.....	52.0	47.0	56.5
Ratio.....	71	72
I2-C dias.....	24.5
C-P2 dias.....	45.0
Palate, M1...	26.0	25.0

Prosthennops serus (?) (Cope)

Material—Calif. Inst. Tech. Coll. Vert. Pale., Nos. 610, the front portion of a mandible with incisor and canine alveoli present and with left P2–M2, but right cheek teeth badly broken; 1936, fragment of a left maxilla with DM2–4, M1, also a right M1.

Horizon—Rome formation, middle Pliocene.

Locality—Calif. Inst. Tech. Vert. Pale. Loc. 62, Rome, Owyhee River, Malheur County, Oregon.

Description and comparison—The mandible, No. 610, is so very much like the type mandible of *Prosthennops serus* that it seems advisable to refer this Rome material to Cope's species, rather than to create a new species for it. As shown by the alveoli, the Rome mandible had very large first and second incisors, as is the case in the type mandible of *Prosthennops serus*, and the third incisor was very small, a further resemblance to the same type. In both the type and referred specimens the canines were very large and robust. The canine-premolar diastema is practically of the same length in both mandibles, and the cheek teeth, not only in size but also in form, are extraordinarily similar in the two specimens. In the jaw from Rome the anterior and external cingula of the premolars, although small, are noticeably larger than are the same structures in the type mandible of *Prosthennops serus*. This would appear to be the principal difference found in the teeth, and might easily be accounted for on the basis of individual variation. As to the jaws themselves, the symphysis of the Rome specimen is slightly heavier than is the symphysis of the type mandible, a development correlative with the robust canines in the Oregon jaw. In both specimens the horizontal rami are very heavy and deep. In the specimen from Rome there is a well-defined shelf along the posterior border of the symphysis, presumably for the insertion of the digastricus muscle. This structure is to be seen in the type mandible, but it is much smaller than in No. 610.

The isolated lower tooth is here considered a first molar rather than a fourth premolar, because the anterior and posterior cusps are of subequal height. As in the teeth of No. 610, there is a well-developed anterior cingulum.

The deciduous teeth are rather well preserved in the maxillary fragment, No. 1936. The anterior two deciduous molars are worn so that their cusps are for the most part obliterated. They are elongated teeth, having narrow anterior portions and wider posterior portions. The fourth deciduous molar is, of course, a replica of the first permanent molar. In these teeth there are well-developed anterior and posterior cingula, in which respect they resemble the palate from the upper Snake Creek beds of Nebraska, Amer. Mus. No. 17582, referred by W. D. Matthew to *Prosthennops serus*. There is no external cingulum in the first upper molar of the California specimen.

All the specimens from the Pliocene deposits exposed near Rome, Oregon, seem to be closer to *Prosthennops serus* than to any other species of the genus. The mandible, especially, is very close to the type mandible of *Prosthennops serus*, as was shown above. Of course, the fact must be recognized that the Rome beds may be slightly younger than the Republican River deposits, in which the type of *Prosthennops serus* was discovered. Since, however, we do not know the exact time range of the Republican River beds, particularly of the deposits in which *Prosthennops serus* occurred, which makes it impossible to postulate definitely whether the type is older than or of the same age as the Oregon specimen, and since there is such a remarkable resemblance between the specimens from the two localities, the view that No. 610 is referable to *Prosthennops serus* is regarded as the most

conservative and most practical solution of the problem presented by its identification.

Comparative measurements are given in the accompanying table.

Comparative measurements (in millimeters) of Prosthennops serus (?) and Prosthennops serus

	<i>P. serus</i> (?) C. I. T. No. 610		<i>P. serus</i> A. M. No. 8511, type	
Length, II-P $\bar{4}$, inclusive.....	121.0		123.0	
Length, C-P diastema.....	50.0		49.0	
Length, symphysis	82.0		83.0	
Width, symphysis (narrowest).....	34.5		31.0	
Length, premolar series.....	39.0		39.0	
	L.	W.	L.	W.
II, at alveolus.....	9.0	4.5	9.0	6.0
I $\bar{2}$, at alveolus.....	7.0	5.0	7.5	7.0
I $\bar{3}$, at alveolus.....	3.5	2.5	2.0	2.0
C at alveolus.....	15.0	13.5	17.0	13.0
P $\bar{2}$	11.0	7.0	11.0	7.0
P $\bar{3}$	12.5	9.0	13.0	9.5
P $\bar{4}$	14.5	12.0	15.0	12.5
M $\bar{1}$	14.5	12.0	15.5	12.0
M $\bar{2}$	17.5	14.0	20.0	15.5
M $\bar{3}$			25.0	15.5
	C. I. T. No. 1936		A. M. No. 17582 (ref.)	
	L.	W.	L.	W.
DM $\bar{2}$	10.5	7.5
DM $\bar{3}$	12.5	10.5
DM $\bar{4}$	13.0	12.5
M $\bar{1}$	16.0	14.0	13.0	13.0

Prosthennops sp.

Material—Calif. Inst. Tech. Coll. Vert. Pale., Nos. 1933, fragments of right and left maxillaries, with right P $\bar{3}$ –M $\bar{2}$ and left P $\bar{2}$ –M $\bar{1}$; 1934, left P $\bar{3}$ – $\bar{4}$, M $\bar{2}$ – $\bar{3}$; 1935, left M $\bar{3}$.

Horizon—Thousand Creek formation, middle Pliocene.

Locality—Calif. Inst. Tech. Vert. Pale. Loc. 63, Thousand Creek, north-western Nevada.

Description and comparison—The upper teeth, No. 1933, are relatively small, in fact they appear to be smaller than the upper teeth in any of the described species of *Prosthennops*, except *Prosthennops kernensis*. Even in this case, the teeth from Thousand Creek are smaller than the type molars of the new species from California, described above, but they are closely comparable in size with those in a paratype palate of *Prosthennops kernensis*, No. 233. On the other hand, the lower teeth, No. 1934, are fully

as large as the corresponding teeth in various species of *Prosthennops*. In view of these size differences, shown by associated specimens, and in view of the fact that *Prosthennops kernensis* demonstrates that there may be a considerable range of size in a single species of *Prosthennops*, it appears logical to suppose that the teeth from Thousand Creek are representative of one species.

The second upper premolar is rather small—considerably smaller than the same tooth in *Prosthennops kernensis* and *Prosthennops oregonensis*, and somewhat comparable in size with the second premolar of *Prosthennops niobrarensis*, a species recently described from Nebraska (Colbert, 1935). This tooth is of triangular shape, as compared with the quadrate P2 of *Prosthennops kernensis*, and in this respect might be considered as less advanced than the second premolar of the Kern River species. On the other hand, the third and fourth premolars of the Thousand Creek specimen are well advanced toward a molariform pattern, and the last premolar, particularly, shows its progressive character in possessing three transverse cusps that constitute its posterior portion. This latter development is a common feature in *Prosthennops*, exhibited by most of the species of the genus, but peculiarly absent in *Prosthennops edensis* from the middle Pliocene of California. The upper molars of the Thousand Creek specimen are of the usual form; the first molar is very much worn, and the second molar shows two transverse pairs of cusps, and anterior and posterior cingula.

The single upper third molar, No. 1935, is comparatively small and relatively short and broad. Its posterior portion is almost as broad as the anterior part of the tooth, a distinct contrast to the upper third molar in *Prosthennops kernensis*.

As was mentioned above, the lower molars, No. 1934, are appreciably larger than the upper teeth from the same horizon. They are rather hypsodont, and in many ways closely comparable with the lower cheek teeth of *Prosthennops kernensis*. The last two premolars are rather narrow as compared with their length, and submolariform. Naturally, the fourth premolar is farther advanced toward acquisition of a molariform pattern than is the tooth preceding it. In both of these teeth, as is typical of *Prosthennops*, the anterior pair of cusps is higher than the posterior pair. The second and third molars are of characteristic *Prosthennops* form and need no special description. The second lower molar consists of the usual four cusps, with an anterior and a posterior cingulum, and a small intermediate cusp in the central valley. In the last molar the anterior cingulum is quite small and the heel is well developed.

These specimens from Thousand Creek have not been assigned a definite specific name because of their fragmentary nature. They are probably specifically identical with the *Prosthennops* material from Thousand Creek described by Merriam in 1911 and by Merriam and Stock in 1928. In No. 1933 the second upper premolar is small and of triangular shape, being composed of only two well-developed cusps, in which respect it is similar to the P2 (U. C. 11876) described by Merriam in 1911. In contrast to this type of premolar is the relatively large three-cusped P2 (U. C. 30040) from Thousand Creek described by Merriam and Stock in 1928. Yet this latter

tooth, in spite of its large size, is still of triangular shape, as compared with the more quadrate P₂ in *Prosthennops kernensis*.

In No. 1933 the third upper premolar is more advanced than this tooth in the other Thousand Creek specimens, cited above. It is quite definitely quadrate, with a large postero-internal cingular cusp, as compared with the more generally tricuspid condition of the previously discovered Thousand Creek specimens.

The fourth upper premolar of No. 1933 is closely comparable with the same tooth in U. C. 30040, not only as regards size, but also as to the development of the two anterior cusps and the three posterior cusps.

*Measurements (in millimeters) of Prosthennops sp. from
Thousand Creek*

	C. I. T. No. 1933		U. C. No. 11876 *		U. C. No. 30040 †			C. I. T. No. 1934	
	L.	W.	L.	W.	L.	W.		L.	W.
P ₂	9.0	8.0	10.0	8.4	9.3	10.0	P ₃	14.0	10.0
P ₃	9.5	10.5	11.2	10.8	10.9	11.1	P ₄	11.5	8.0
P ₄	11.0	12.5	12.2	12.5			
M ₁	14.0	12.5	M ₂	17.0	13.0
M ₂	16.5	15.0	M ₃	24.5	13.5
	C. I. T. No. 1935								
	L.	W.							
M ₃	17.5	14.0							

* After Merriam, 1911.

† After Merriam and Stock, 1928.

The last upper molar figured in the 1911 paper would seem to be somewhat longer than the comparable tooth in the present collection (No. 1935), and more like the same tooth in *Prosthennops kernensis*. Thus it may be seen that there are certain differences of detail among the several specimens of *Prosthennops* from the Thousand Creek formation. Whether these differences are of specific significance is a question that cannot at present be determined. For the time being it would seem best to consider these several specimens from Thousand Creek as probably referable to a single

Platygonus sp.

J. R. Schultz, A Late Cenozoic Vertebrate Fauna from the Coso Mountains, Inyo County, California. Carnegie Inst. Wash. Pub. No. 487, 101-102, pl. 8, figs. 4-6, 1937.

Material—Calif. Inst. Tech. Coll. Vert. Pale., No. 1850, mandibular symphysis with incisors and canines; also right and left lower first molars and lower third molars.
species.

Horizon—Coso formation, upper Pliocene.

Locality—Calif. Inst. Tech. Vert. Pale. Loc. 131, Coso Mountains, California.

Description and comparison—John R. Schultz has recently described this material in the publication cited above. A few additional observations may be made. The symphysis and isolated lower teeth from Coso Mountains are definitely referable to the genus *Platygonus*. The symphysis is somewhat differently shaped from that of typical *Prosthennops*, being relatively broad and shallow, in which respect it exhibits a feature characteristic of *Platygonus*. Three lower incisors are present, of which the third one is rather large. The broken canines seem to have been quite long, as might be expected in *Platygonus*.

The molars give the clearest indication that the peccary from the Coso Mountains is related to the genus *Platygonus*. The teeth are hypsodont, strongly cross-crested, and lack either well-developed cingula or accessory cusps. The two first molars are worn, so that the transversely placed cusps are connected by their inner wings, making the tooth bilophodont. In the third molar the cusps are unworn and distinct and show the typical *Platygonus* structure. The heel of this tooth is large.

Platygonus bicalcaratus and *Platygonus texanus* are found in the Blanco formation of Texas, giving strong evidence that this genus was well established in the upper Pliocene, even though it did not reach the culmination of its development until the Pleistocene. In the Pacific Coast region, Frick has described some canine teeth from the Eden beds, which he referred to *Platygonus*. Other occurrences of this genus in the Pliocene have been occasionally reported (Merriam, 1915, 1917, Etchegoin [probably *Prosthennops*]; Matthew, 1909, "Fort Niobrara"="Nebraska"=Valentine, generic reference and horizon questioned).

Measurements (in millimeters) of Platygonus sp.

	C. I. T. No. 1850
Length of symphysis.....	82.0
Breadth of symphysis (mid portion).....	33.0
Depth of symphysis.....	25.0
I ¹ length	5.0
width	5.7
I ² length	6.0
width	6.5
I ³ length	4.6
width	5.2
C length	18.8
width	12.0
est. height above alveolus.....	60.0
M ¹ length	14.0
width	10.0
M ³ length	25.0
width	13.3
height	12.0

SPECIFIC CHARACTERS IN TEETH OF PROSTHENNOPS

Of the North American species of *Prosthennops*, eight, including the two new forms described in this paper, are based on adequate material. They may be listed as follows:

1. *Prosthennops crassigenis* Gidley, generic type
2. *Prosthennops serus* (Cope)
3. *Prosthennops edensis* Frick
4. *Prosthennops longirostris* Thorpe
5. *Prosthennops xiphodonticus* Barbour
6. *Prosthennops niobrarensis* Colbert
7. *Prosthennops kernensis*, new species
8. *Prosthennops oregonensis*, new species

Of these, only the first is known from a complete skull. Numbers 2 and 6 are known from partial skulls, and in No. 2 the skull is that of a referred specimen. The remaining species are based on palates and jaws with more or less complete dentitions. Thus the only characters common to the several species of *Prosthennops* are to be found in the teeth.

Unfortunately, the teeth in *Prosthennops* (as is the case among so many of the Artiodactyla) are strikingly alike in all the different forms, making the differentiation of species an exceedingly difficult task. Consequently it is necessary to base the specific differences in this genus upon very slight but constant characters in the dentition, characters that are not too greatly affected by factors of individual variation. But until the present study was undertaken, the several species of *Prosthennops* were known only from isolated specimens, and therefore data were lacking as to the amount of individual variation that occurred in any one species.

The present studies have indicated the degree of variability in teeth of one species of *Prosthennops*, namely *Prosthennops kernensis*, and indicate to a certain extent the dental characters that are constant enough to be valuable for specific distinctions within the genus.

That certain relatively small differences in the teeth are of real specific value would seem evident from a comparison of the dentitions in forms having the skulls preserved. That is, the skulls of *Prosthennops crassigenis*, *Prosthennops serus*, and *Prosthennops niobrarensis* clearly indicate that slight but constant differences in the dentition are accompanied by very striking differences in the skulls. Therefore this evidence, combined with the fact that most of the several forms of *Prosthennops* come from different stratigraphic horizons in the upper Miocene and in the Pliocene, and from widely separated localities (which considerations in themselves would constitute almost *a priori* justification for specific differentiation), seems to offer

sufficient reason for separating the species in the genus on slight but constant dental characters.

Naturally the question arises as to just what are the constant specific differences in the teeth of *Prosthennops*. This question may be answered more or less satisfactorily by a recognition of the extent of variation in the dentition of *Prosthennops kernensis* and by a comparison of the variable characters in this species with similar characters in other species of the genus.

General size differences do not constitute valid distinctions among the several species of the genus. As may be seen in the accompanying graphs (figures 3 and 4), the size differences in the cheek teeth of *Prosthennops* are considerable but cannot be correlated. That is, no one species stands out as uniformly larger than any other species, and, with the exception of *Prosthennops xiphodonticus*, no one species may be distinguished as uniformly smaller than any of the other species. Moreover it is to be noted that the size variation in a single species, *Prosthennops kernensis*, constitutes in almost all cases a very considerable fraction of the size variation in the genus. It is at once quite apparent that if we had series of dentitions of the various species of *Prosthennops*, similar to our series for *Prosthennops kernensis*, the size variations among individuals of the several species would be so inextricably mixed as to effect a complete effacement of specific distinctions based on size alone.

It must be remembered, however, that the differences in size between certain teeth, such as the incisors and the second premolars, may to a limited degree constitute good specific characters. Even so, it becomes evident that distinctions between species of *Prosthennops*, as seen in the dentition, must be based mainly on observable characters rather than on measurable size differences. An evaluation of the tooth characters in the various species of *Prosthennops*, based on a comparative study of these species and on a study of individual variation within one form, *Prosthennops kernensis*, seems to indicate that certain details of structure are to a limited extent of diagnostic value. These characters, which must be used with care, are as follows:

Upper dentition

Lower dentition

a. Relative size of first and second incisors

b. Presence or absence of third incisor

c. Robust or flat canine

d. Size and shape of second premolar

e. Molarization of premolars

f. Relative breadth of molars

g. Development of cingula on molars

h. Relative width of posterior part of

M₃

b. Relative size of third incisor

c. Robust or flat canine

e. Molarization of premolars

f. Relative breadth of molars

h. Development of talonid in M₃

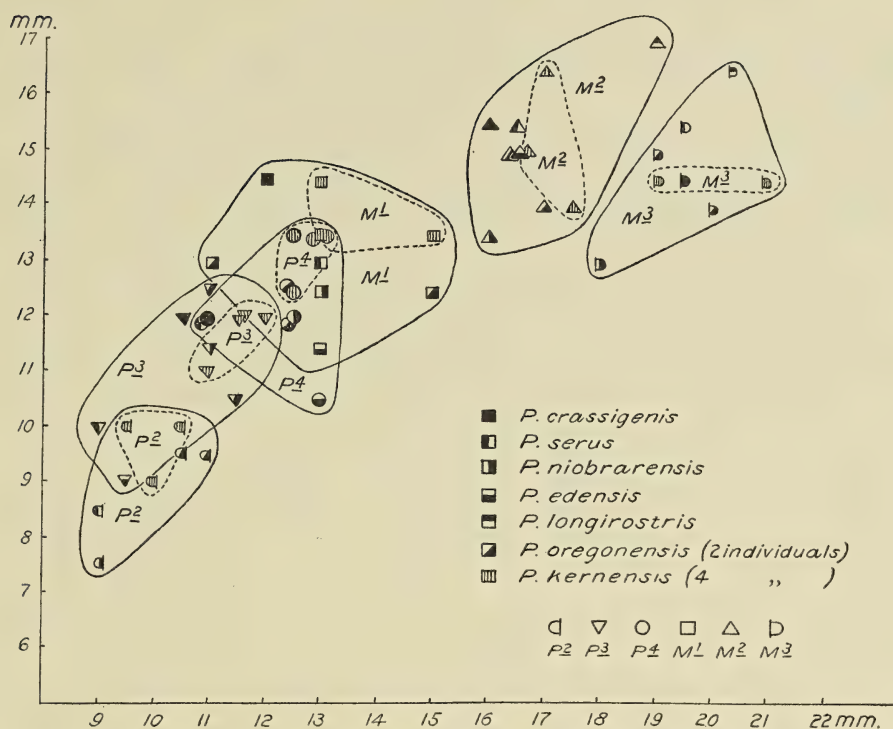


FIG. 3—Graph to show the variation in the upper cheek teeth of seven species of *Prosthennops*. Solid lines enclose dimensional limits for the genus. Dotted lines enclose limits of variation for *Prosthennops kernensis*. Lengths on horizontal axis, widths on vertical axis.

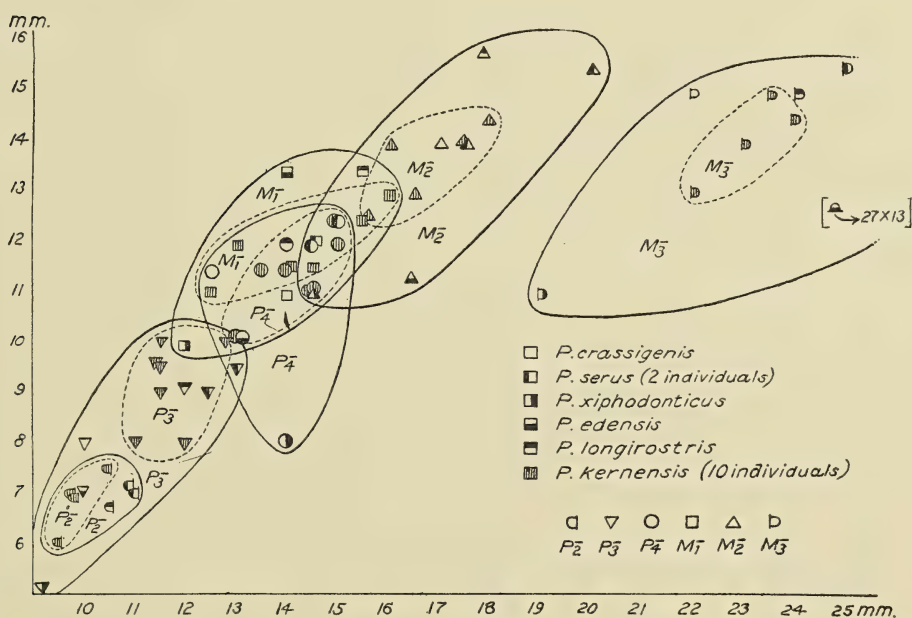


FIG. 4—Graph to show the variation in the lower cheek teeth of six species of *Prosthennops*. Solid lines enclose dimensional limits for the genus. Dotted lines enclose limits of variation for *Prosthennops kernensis*. Lengths on horizontal axis, widths on vertical axis.

Comparison of Dental Characters in Species of *Prosthennops*

Species	Size of I ₁ and I ₂	Presence or absence of I ₃	C index		Size of P ₂	Molarization of PM's (p=partial)	Breadth of molars U./L.	Cingula on molars U./L.	Width of posterior portion of M ₃ /talonid of M ₃
			U.	L.					
<i>P. crassignis</i> type (ref.)	Small	Absent	75	$\frac{3}{3p} \frac{4}{4}$	Broad Broad	? Absent	Broad Broad
<i>P. serus</i> type (ref.)	Large	Absent	65	88	Small	$\frac{3}{3} \frac{4}{4}$	Broad Broad	Present Absent	Broad Broad
<i>P. serus</i> (Owyhee)	82	$\frac{3}{3} \frac{4}{4}$ Broad Absent
<i>P. edensis</i>	$\frac{3}{3} \frac{4}{4}$	Broad	Absent Absent
<i>P. longirostris</i>	Absent	$\frac{3}{3} \frac{4}{4}$	Medium Medium	Present Absent	Broad Broad
<i>P. xiphodonticus</i>	Small	$\frac{4}{4}$	Narrow	Narrow
<i>P. niobrarensis</i>	Medium	Present	47	Small	$\frac{3}{3} \frac{4}{4}$	Narrow	Absent	Narrow
<i>P. kernensis</i>	57	75	Medium	$\frac{2p}{3} \frac{3}{4} \frac{4}{4}$	Medium Narrow	Absent Absent	Narrow Broad
<i>P. oregonensis</i>	Large	Absent	60	Large	$\frac{3}{3} \frac{4}{4}$	Broad	Absent	Broad
<i>P. sp.</i> (Thousand Creek)	Small	$\frac{3}{3} \frac{4}{4}$	Medium	Absent	Broad
South American species:
<i>P. doellojuradoi</i>	Large	Absent	Large	$\frac{3}{3p} \frac{4}{4}$	Broad Broad	Absent Absent	Broad Narrow
<i>P. valentini</i>	Broad	Absent

In the above list, all the characters are naturally affected by factors of individual variation, *b*, *c*, *g*, and to some extent *h*, particularly so. Moreover, *c* is greatly affected by sexual dimorphism, probably so much so as to make its use in specific determinations of little value. Lastly, *f* is affected by wear.

The accompanying table shows the way in which the several species of *Prosthennops* may be separated from one another on the basis of dental characters. It is evident that no species is just like another species in its dental features, but on the other hand no great differences are to be seen in the teeth of the various species.

Prosthennops crassigenis and *Prosthennops serus* are similar by reason of their very broad, heavy cheek teeth. In this respect, too, *Prosthennops edensis* may be compared with the above forms. *Prosthennops xiphodonticus* is very small, with "primitive" nonmolariform premolars. *Prosthennops kernensis* is strikingly similar to *Prosthennops niobrarensis* by reason of the configuration and relative narrowness of the cheek teeth. In like manner but to lesser extent *Prosthennops oregonensis* and *Prosthennops longirostris* are like the two forms last mentioned and like each other. They show differences, however, that separate them as valid species; these differences may be readily seen by an examination of the table.

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PLATE 1

Prosthennops kernensis, n. sp.

FIG. 1—Skull fragment with left P₂-P₄, No. 553, ventral view.

FIGS. 2, 2*a*—Mandibular fragment with left DM₃-MI, No. 225, lateral and occlusal views.

FIG. 3—Type specimen, palate with cheek teeth, No. 224, ventral view.

FIG. 4—Left metatarsal IV, No. 234, anterior view.

FIG. 5—Left calcaneum and astragalus, No. 230.

FIG. 6—Left metacarpal III, No. 237, posterior view.

Figs. 1 and 3, $\times \frac{2}{3}$; figs. 2, 2*a*, 4-6, $\times 1\frac{1}{3}$.

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Kern River Pliocene, California.



PLATE 2

Prosthennops kernensis, n. sp.

FIG. 1—Right $M\bar{3}$, No. 240a.

FIG. 2—Right $P\bar{3}$ – $P\bar{4}$, No. 240.

FIGS. 3, 3a—Fragment of right ramus with $DM\bar{2}$ – $DM\bar{4}$, No. 1938.

FIG. 4—Left $P\bar{3}$ – $M\bar{3}$, No. 545.

FIG. 5—Right $M\bar{3}$, No. 2141.

FIG. 6—Right ramus with $P\bar{2}$ – $M\bar{3}$, No. 241.

FIG. 7—Right ramus with $P\bar{4}$, $M\bar{1}$ – $M\bar{2}$, No. 236.

FIG. 8—Fragment of left ramus with $P\bar{2}$ – $M\bar{3}$, No. 227.

FIG. 9—Fragment of left ramus with $M\bar{1}$ – $M\bar{3}$, No. 226.

Occlusal views, except fig. 3, which represents specimen in side view.

Figs. 1–7, $\times 1\frac{1}{3}$; figs. 8 and 9, $\times \frac{2}{3}$.

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Kern River Pliocene, California.



PLATE 3

Prosthennops kernensis, n. sp.

- FIGS. 1, 1*a*—Fragment of right ramus with DM $\overline{3}$ –DM $\overline{4}$, No. 1937, lateral and occlusal views.
- FIGS. 2, 2*a*—Fragment of left ramus with DM $\overline{4}$, No. 1939, lateral and occlusal views.
- FIGS. 3, 3*a*—P $\overline{2}$, No. 2142, lateral and occlusal views.
- FIG. 4—Right P $\overline{3}$ –P $\overline{4}$, No. 551, occlusal view.
- FIGS. 5, 5*a*—Fragment of left ramus with P $\overline{3}$ –P $\overline{4}$, M $\overline{1}$, and part of M $\overline{2}$, No. 228, lateral and occlusal views.
- FIGS. 6, 6*a*—Right ramus with deciduous incisors, canine, and cheek teeth, No. 2038, lateral and superior views.

All figures $\times 1\frac{1}{3}$.

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Kern River Pliocene, California.

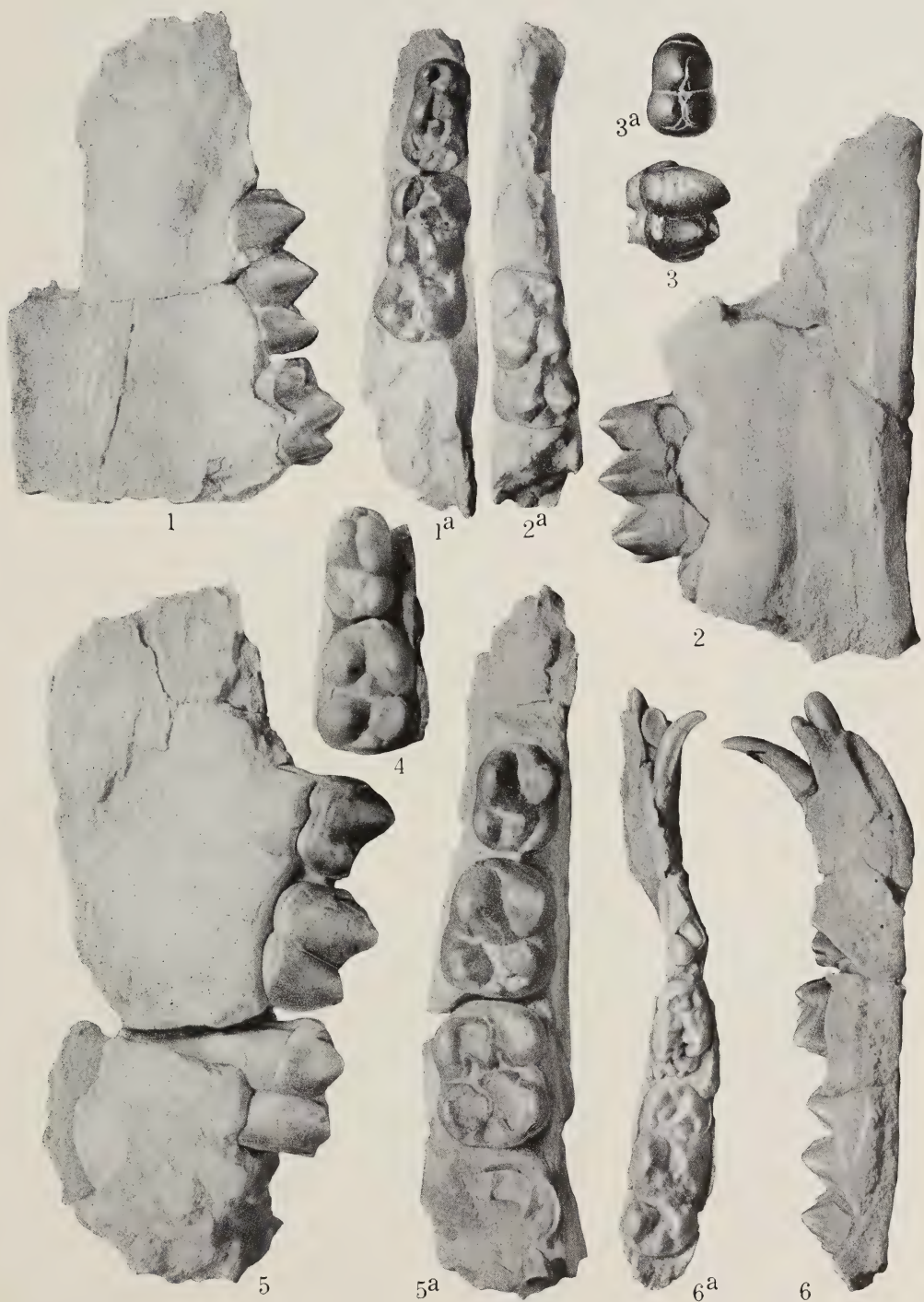


PLATE 4

Prosthennops kernensis, n. sp.

- FIGS. 1, 1a—Mandibular symphysis with canines, No. 548, lateral and superior views.
FIGS. 2, 2a—Portion of left premaxilla and maxilla with canine, No. 239, lateral and ventral views.
FIGS. 3, 3a—Mandibular symphysis with incisors and canine, No. 229, superior and lateral views.
FIGS. 4, 4a—Mandibular symphysis with incisors and canine, No. 1940, lateral and superior views.

Figs. 1-3a, $\times \frac{2}{3}$; figs. 4 and 4a, $\times 1\frac{1}{3}$.

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Kern River Pliocene, California.



PLATE 5

Prosthennops sp.

FIGS. 1, 1*a*—Fragment of right and left maxillaries with superior cheek teeth, No. 1933.

FIG. 2—Left M₃, No. 1935.

FIG. 5—Left P₃–P₄, M₂–M₃, No. 1934.

Occlusal views. Figs. 1 and 1*a*, $\times \frac{2}{3}$; figs. 2 and 5, $\times 1\frac{1}{3}$.

Thousand Creek Pliocene, Northwestern Nevada.

Prosthennops oregonensis, n. sp.

FIG. 4—Type specimen, palate with superior dentition, No. 535.

FIG. 3—Paratype, palate with cheek teeth, No. 533.

Ventral views. $\times \frac{2}{3}$.

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Rattlesnake Pliocene, Eastern Oregon.



1



1^a



3



2



4



5

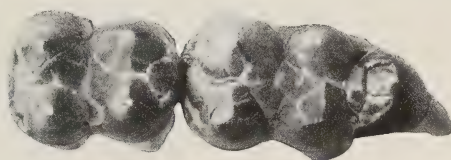


PLATE 6

Prosthennops kernensis, n. sp.

FIG. 1—Fragment of left ramus with $\overline{P2}$ – $\overline{M3}$, No. 231, occlusal view, $\times \frac{2}{3}$.

FIG. 2—Fragment of right ramus with $\overline{P2}$ – $\overline{P3}$, No. 547, occlusal view, $\times 1\frac{1}{3}$.

Kern River Pliocene, California.

Prosthennops serus (?) (Cope)

FIG. 3—Fragment of left maxilla with $\overline{DM2}$ – $\overline{DM4}$, $\overline{M1}$, No. 1936, ventral view.

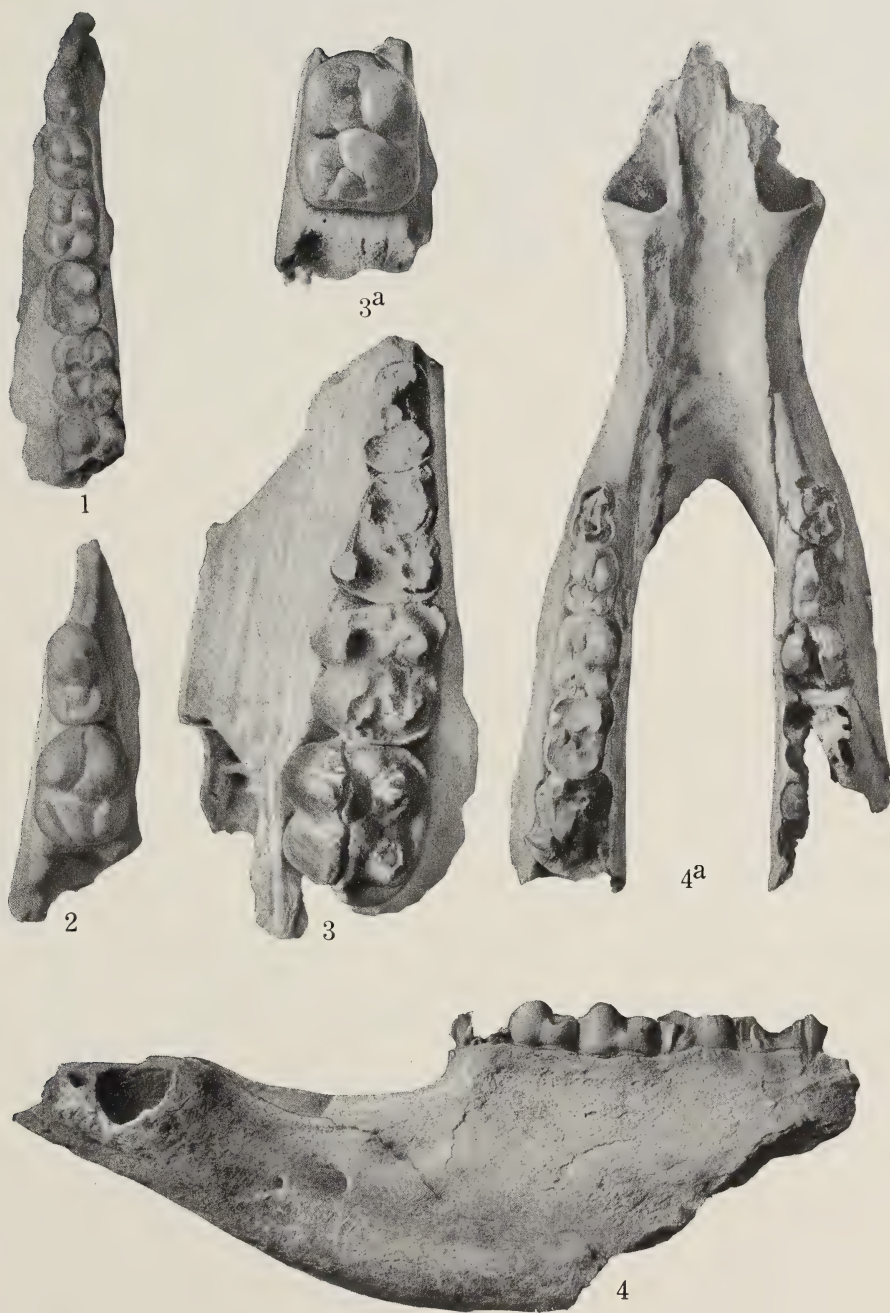
FIG. 3a—Right $\overline{M1}$, No. 1936a, occlusal view.

FIGS. 4, 4a—Front portion of mandible with incomplete dentition, No. 610, lateral and superior views.

Figs. 3 and 3a, $\times 1\frac{1}{3}$; figs. 4 and 4a, $\times \frac{2}{3}$.

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Rome Pliocene, Malheur County, Oregon.



CONTRIBUTIONS TO PALÆONTOLOGY

VII

PLANTS IN THE DUNG OF NOTHROTHERIUM FROM
RAMPART AND MUAV CAVES, ARIZONA

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With eleven plates and one text-figure

[Issued May 6, 1938]

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PLANTS IN THE DUNG OF NOTHROTHERIUM FROM RAMPART AND MUAV CAVES, ARIZONA

INTRODUCTION

In the summer of 1933 the writers, at the suggestion of Dr. Chester Stock of the California Institute of Technology, made a complete examination of the plant remains composing the dung-balls of the ground sloth *Nothrotherium* from Gypsum Cave, Nevada.

The results of this study proved that the plant assemblage represented in the diet of *Nothrotherium* when it lived at Gypsum Cave was a typical desert flora of higher altitudes. The plant assemblage was in every respect similar to the flora growing today at a locality in the Clark Mountains of California, 42 miles distance from the cave. In this locality, which is at a higher elevation and consequently in a considerably less arid region, *Yucca brevifolia*, *Yucca baccata*, *Yucca mohavensis*, *Agave utahensis*, and *Ephedra nevadensis* grow abundantly.

Since some of the types most abundant in the dung-balls, such as *Y. brevifolia* and *Y. baccata*, as well as *A. utahensis*, do not occur in the vicinity of Gypsum Cave at present, it was concluded that at the time the ground sloths inhabited the cave the climate was more moist than at present.

The results of this work, as well as the methods employed in making the determinations on the plant tissues found, are embodied in a report published by the Carnegie Institution of Washington.¹

After completing the investigation of the Gypsum Cave material, with the exception of a few identifications made for Mr. Edgar B. Howard of the University of Pennsylvania on sloth dung from New Mexico, the writers did no further work on sloth-dung floras until late in the spring of 1937, when requested to examine samples, presumably of the dung of *Nothrotherium*, from a newly discovered locality in Arizona, that of Rampart Cave. This was material sent to Dr. Chester Stock by the officials of the United States National Park Service at Boulder City, Nevada, who were engaged at that time in the excavation of the deposit.

A preliminary examination of the material showed that while texture, size, and degree of preservation of the dung-balls exactly resembled these features observed in the Gypsum Cave specimens, there was a marked dissimilarity in the plant assemblage represented by the dried tissue present.

¹ J. D. Lauder milk and Philip A. Munz, Carnegie Inst. Wash. Pub. No. 453, IV, 1934.

where this meets the nearly vertical scarp of the canyon wall. The elevation of Rampart Cave is approximately 700 feet above the river (plate 1).

The caves, which have been only partly excavated (1937), were discovered by Willis Evans of the National Park Service in the summer of 1936. The region in which the caves occur has heretofore been one of the most inaccessible parts of the Lower Grand Canyon, and it is only from the approach made available by the newly formed Lake Mead that the caves can be reached at the present time.

The floor of Rampart Cave, which extends for some hundreds of feet back into the limestone formation of the canyon wall, is covered with a nearly unbroken layer of sloth dung (plate 3). Excavations conducted by the National Park Service workers show this layer to be in places six feet or more in thickness. The remains of several sloths, including skeletal elements, integument, and hair, have been recovered from the dung layer.

Owing to the extreme dryness of the cave and perhaps to other causes, the dung layer is in a perfect state of preservation and, except in places where the work of the excavators has disturbed the deposit, this is much as it was when the cavern was abandoned by the last ground sloth.

Samples of dung were collected from both caves. The locations of the samples collected at Rampart Cave are shown on the accompanying map. No map was available for Muav Cave, but samples collected from near the entrance were found to be of special importance since these were the only dung-balls in which yucca tissue was present. Muav Cave is much nearer the river than is Rampart and has been occupied by Indians. The sloth-dung deposit has been much disturbed, so that there is now very little present.

STUDY OF EXISTING FLORAS

It was found in the case of the Gypsum Cave investigations that for best results, plant specimens collected for microscopic comparison with the plant remains in the dung should be killed and fixed in the field, since dried specimens, even after maceration, are apt to present features which are sometimes misleading. This is particularly true of certain grasses and plants like *Nolina*, in which types the stomates lie at the bottom of the parallel rifts between the veins.

Lynds Jones mixture (formalin-alcohol) was used for killing and fixing, since material treated by this method can be left in the solution until ready for use. About forty specimens were collected from the two localities.

Altogether, a considerable number of species were identified in the vicinity of the two caves, fifty-six being observed on the trail from

the river to Rampart Cave and forty-four on the trail to Muav Cave. In some cases the identifications had to be made from dead plants or old ones that had shed their flowers, and the exact species could not be determined. A list of the species found is given at the end of this paper.

While the general region about the caves is very arid, the vegetation is more abundant than is the case at Gypsum Cave. Moreover, the canyon wall has occasional seeps and springs, such as the one on the trail between the river and Muav Cave, and those a short distance up the river at Emery Falls Canyon, where there is rank vegetation including such species as *Adiantum Capillus-Veneris*, *Phragmites communis*, and *Prosopis chilensis*. Cane arrow shafts (*Phragmites*), as well as numerous mesquite quids (*Agave*) and corn husks and cobs from Muav Cave probably date from only a comparatively remote Indian occupancy.

The type slides of the alcoholic material were prepared as a preliminary operation before beginning the comparisons with the tissues recovered from the dung. The type material included transverse and longitudinal sections of stems, leaves, and petioles, sections of epidermal tissue, hairs, spines, and pollen. Both temporary and permanent preparations were made. In all essentials this work was a repetition of the course followed in our previous report.¹

In many cases the work required that numerous mounts be made from the same organ since it had been found in previous investigations that the disposition of the stomates, hairs, etc. varied to an important extent with different areas of the same leaf or stem.

MACROSCOPIC DESCRIPTION OF THE SLOTH DUNG

The ejecta, when in unbroken masses, occur as roughly cylindrical blocks or lumps composed of flattened smaller balls (plate 3). The surface is covered with a hard brown coating of dried mucus varnish. In several specimens this has a distinctly reddish color. Some of the reddish coating was removed and to such samples the benzidine test for hemoglobin was applied. The results were negative in all cases. As a result of this observation it was concluded that while the stain may have resulted from blood, the latter had been so altered by oxidation and by other causes as no longer to give any reactions for blood, or else that the red color has resulted from undetermined change, probably both chemical and bacterial, in the mucus coating.

Broken balls show that these are composed of compact fibrous masses of desiccated vegetable tissue. Unlike the dung-balls from Gypsum Cave, in which large pieces of the tough epidermis of *Yucca*

¹ J. D. Lauder milk and Philip A. Munz, Carnegie Inst. Wash. Pub. No. 453, IV, pp. 32, 33, 1934.

are abundant, the Rampart and Muav samples show that *Yucca* occurs but rarely. Observation with a hand lens shows that the dung-balls in these cases are composed largely of fragments of the stems of *Ephedra*; the sharp, blackish spine-like tips of *Ephedra* branches are common.

Much of the material composing the balls is only coarsely trituated and in one case an entire seed of *Prunus* sp.? was recovered from a dung-ball. Some of the samples examined show a distinct variation in the proportions of *Ephedra* material to other tissues. One ball was found to consist largely of grass with much dried mucus or gummy material cementing the fibers together. This sample may represent a pathological condition of the sloth from which it originated, since perfectly preserved nematode worms as well as their eggs were abundant. Neither the worms nor the eggs were viable in incubated extracts of the dung.

Yucca tissues were observable in only two cases examined and these in samples from Muav Cave. The single species present, namely *Yucca mohavensis*, resembles that found in the Gypsum Cave material.

MICROSCOPIC EXAMINATION OF THE DUNG

In addition to the large fragments, which range from pieces of stem 3 or 4 cm. long down to material retained by a 20 mesh screen, there was much fine powder. This fine fraction, which is evident as yellowish dust when a ball is broken, contained many hairs from several species of plants. Among these the hair from the leaves and stems of *Sphaeralcea* was especially abundant. Hair from *Atriplex* was common, as well as pieces of the epidermis of the same plant. The latter material required careful handling to be brought into a recognizable condition. Ordinarily, hairs of *Atriplex* separated from the epidermis appear as almost structureless clumps of tissue, but in preparations purposely somewhat overstained the tubular stems of individual hairs become recognizable; the clumps can then be teased apart and entire hairs disentangled for conclusive identification. Many sporangia as well as spores and fragments of the petioles and epidermis were identified as probably originating from *Adiantum*.

Certain objects which in size, form, and color almost exactly resemble the pollen of *Pinus* occur constantly in the fine fractions. After considerable investigation, these were found to be the guard cells from stomates of *Ephedra*. Because of an apparently more durable composition these have remained entire after disintegration of the remaining cells of the epidermis. It may be remarked here that while *Ephedra* is common in the Gypsum Cave specimens, structures

of this type were not observed. *Opuntia* is represented by spines and fragments of the epidermis. The occurrence of *Opuntia* in this material is a striking point of contrast between the assemblages found in the Rampart and Muav dung and that from Gypsum Cave. In the latter case, although hundreds of preparations of the fines were examined, no indication of cacti was found.

With the exception of two samples from Muav which contain *Yucca*, calcium oxalate crystals of the yucca type were not found.

A type of epidermis having considerable resemblance to that of various grasses and *Phragmites* was eventually identified as probably belonging to *Nolina*. This genus was not actually observed as now growing in the vicinity of either of the caves, but is reported from that general locality.

Pollen grains of several types occur abundantly, but are in general only evident after the fines are first washed with alcohol and acetone for the purpose of removing the resinous deposit which obscures the finer structural details. While much of this pollen is from plants that have been identified on the basis of other tissues, other types of pollen which constantly occur can only be tentatively identified as belonging to *Compositæ* and grasses.

The plants determined do not by any means exhaust the list of species present in the dung-balls. Much material remains unidentified for lack of definite type material for comparison, since, as has previously been mentioned, many of the living plants observed in the Lower Grand Canyon had matured earlier than the time of our visit and were no longer suitable for type material. Furthermore, much of the dung material does not present sufficiently distinctive structures to suggest living plants with which they might be compared.

CONCLUSIONS

From the evidence we conclude that when the ground sloths inhabited Rampart and Muav Caves, the flora and presumably the climate were essentially the same as those of the region today. The fact that arrow shafts and corn cobs occur in Muav Cave appears also to indicate that in times relatively remote the climate was much as it is at present. Although *Nolina* was not observed as a growing plant in the vicinity of the caves, this is not considered a point of much significance since it does occur at localities not many miles from the caves and grows under a similar environment. *Adiantum*, which is relatively abundant not far from the caves and is a common constituent of the dung-balls, points also to a former environment much like the present one in which occasional seeps and springs occur.

TABLE 1—*List of plants observed growing along trail from Colorado River to Rampart Cave, Arizona, June 16, 1937*

1. *Notholaena Parryi* D. C. Eaton—Parry's cloak fern
2. *Ephedra nevadensis* Wats.—Desert tea
3. *Hilaria rigida*—Galleta grass
4. *Aristida Wrightii* Nash—Triple-awned grass
5. *Muhlenbergia Porteri* Scribn.—Bush muhly
6. *Triodia pulchella* HBK.—Fluff grass
7. *Poa Bigelovii* Vasey & Scribn.—Bigelow blue grass
8. *Bromus rubens* L.—Foxtail chess
9. *Yucca Whipplei* Torr.—Our Lord's candle
10. *Parietaria floridana* Nutt.—Pellitory
11. *Eriogonum inflatum* Torr. & Frem.—Desert trumpet
12. *Allionia incarnata* L. var. *villosa* ? (Standl.) Munz
13. *Argemone platyceras* Link & Otto—Prickly poppy
14. *Lepidium lasiocarpum* Nutt.—Peppergrass
15. *Caulanthus lasiophyllus* (H. & A.) Payson—Wild cabbage
16. *Descurainia brachycarpa* (Richardson) O. E. Schulz—Tansy mustard
17. *Draba cuneifolia* Nutt.—
18. *Acacia Greggii* Gray—Cat's-claw
19. *Krameria Grayi* Rose & Painter—
20. *Erodium cicutarium* (L.) L'Her.—Filaree
21. *Larrea divaricata* Cav.—Creosote bush
22. *Sphæralcea ambigua* Gray—Desert hollyhock
23. *Fouquieria splendens* Engelm.—Ocotillo
24. *Eucnide urens* Parry—
25. *Opuntia acanthocarpa* Engelm. & Bigel.—Cholla
26. *Opuntia basilaris* Engelm. & Bigel.—Beaver tail
27. *Cereus Engelmannii* Parry—Hedgehog cactus
28. *Echinocactus acanthodes* Lemaire—Barrel cactus
29. *Oenothera multijuga* Wats.—
30. *Oenothera brevipes* Gray—
31. *Gilia inconspicua* (Smith) Dougl.—
32. *Gilia dichotoma* Benth.—Evening snow
33. *Phacelia* sp.—Wild heliotrope
34. *Phacelia crenulata* Torr.—Wild heliotrope
35. *Coldenia hispidissima* (Torr.) Gray
36. *Amsinckia tessellata* Gray—Fiddle neck
37. *Cryptantha maritima* Greene—White forget-me-not
38. *Cryptantha barbigera* (Gray) Greene—White forget-me-not
39. *Cryptantha pterocarya* (Torr.) Greene—White forget-me-not
40. *Verbena Gooddingii* Briq.—Vervain
41. *Physalis crassifolia* Benth.—Ground cherry
42. *Nicotiana trigonophylla* Dunal.—Wild tobacco
43. *Plantago insularis* var. *fastigiata* (Morris) Jeps.—Plantain
44. *Galium stellatum* Kell. var. *eremicum* Hilend & Howell—
45. *Hofmeisteria pluriseta* Gray—Arrowleaf
46. *Brickellia arguta* Robinson—
47. *Gutierrezia lucida* Greene ?—Match weed
48. *Amphipappus Fremontii* T. & G.—
49. *Aplopappus spinulosus* var. *Gooddingii* (Nels.) Blake—
50. *Aster abatus* Blake—Desert aster

51. *Filago arizonica* Gray—
52. *Franseria dumosa* Gray—Burro weed
53. *Viguiera deltoidea* var. *Parishii* (Greene) Vasey & Rose—
54. *Encelia farinosa* Gray—Incienso
55. *Bebbia juncea* (Benth.) Greene var. *aspera* Greene—Sweet bush
56. *Stephanomeria pauciflora* var. *myrioclada* (D. C. Eat.) Munz ?—Flowering straw

TABLE 2—*List of plants observed on trail from Colorado River to Muav Caves, Arizona, June 17, 1937*

1. *Notholaena Parryi* D. C. Eaton—Parry's cloak fern
2. *Adiantum Capillus-Veneris* L.—Venus-hair fern
3. *Ephedra nevadensis* Wats.—Desert tea
4. *Muhlenbergia Porteri* Scribn.—Bush muhly
5. *Stipa speciosa* Trin. & Rupr.—Desert needle grass
6. *Phragmites communis* Trin.—Common reed
7. *Bromus rubens* L.—Foxtail chess
8. *Agropyron Smithii* Rydb. ?—Bluestem
9. *Yucca Whipplei* Torr.—Our Lord's candle
10. *Atriplex confertifolia* Wats.—Spiny saltbush
11. *Atriplex hymenelytra* (Torr.) Wats.—Desert holly
12. *Suaeda* probably *Torreyana* Wats. var. *ramosissima* (Standl.) Wats.—Seep weed
13. *Tidestromia oblongifolia* (Wats.) Standl.—
14. *Delphinium* sp.—Larkspur
15. *Stanleya pinnata* (Pursh) Britt.—Prince's plume
16. *Caulanthus lasiophyllus* (H. & A.) Pays.—Wild cabbage
17. *Lepidium lasiocarpum* Nutt.—Peppergrass
18. *Thelypodium* of *integrifolium* group—
19. *Draba cuneifolia* Nutt.—
20. *Arabis* sp.—Rock cress
21. *Crossosoma Bigelovii* Wats.—
22. *Acacia Greggii* Gray—Cat's-claw
23. *Prosopis chilensis* (Molina) Stuntz—Mesquite
24. *Larrea divaricata* Cav.—Creosote bush
25. *Sphaeralcea ambigua* Gray—Desert hollyhock
26. *Fouquieria splendens* Engelm.—Ocotillo
27. *Opuntia basilaris* Engelm. & Bigel.—Beaver tail
28. *Echinocactus acanthodes* Lemaire—Barrel cactus
29. *Oenothera multijuga* Wats.—
30. *Phacelia* sp.—
31. *Amsinckia tessellata* Gray—Fiddle neck
32. *Cryptantha pterocarya* (Torr.) Greene—White forget-me-not
33. *Cryptantha maritima* Greene—White forget-me-not
34. *Nicotiana trigonophylla* Dunal.—Wild tobacco
35. *Lycium* sp.—Box thorn
36. *Plantago insularis* var. *fastigiata* (Morris) Jeps.—Plantain
37. *Galium stellatum* Kell. var. *eremicum* Hilend & Howell
38. *Aplopappus spinulosus* var. *Gooddingii* (Nels.) Blake—
39. *Hofmeisteria plurisetia* Gray—Arrowleaf
40. *Erigeron divergens* T. & G.—
41. *Solidago sparsiflora* Gray—Goldenrod

42. *Aplopappus acradenius* var. *eremophilus* (Greene) Munz—
 43. *Franseria dumosa* Gray—Burro weed
 44. *Viguiera deltoidea* var. *Parishii* (Greene) Vasey & Rose—
 45. *Cirsium undulatum* (Nutt.) Spreng.—Thistle

TABLE 3—*Comparative list of plants from northwestern Arizona*

Species	Rampart & Muav	Sloth dung	
	Cave vicinity	Rampart	Muav
1. <i>Ephedra nevadensis</i> Wats.....	X	X	X
2. <i>Adiantum Capillus-Veneris</i> L.....	X	X	X
3. <i>Aristida Wrightii</i> Nash.....	X	X sp.	X sp.
4. <i>Phragmites communis</i> Trin.....	X	X	X
5. <i>Nolina Bigelovii</i> Torr.....	?	X sp.	X sp.
6. <i>Yucca mohavensis</i> Sarg.....	?	X
7. <i>Atriplex hymenelytra</i> (Torr.) Wats....	X	X sp.	X sp.
8. <i>Atriplex confertifolia</i> Wats.....	X	?	?
9. <i>Cassia Covesii</i> Gray.....	X	X sp.
10. <i>Larrea divaricata</i> Cav.....	X	X	X
11. <i>Sphæralcea ambigua</i> Gray.....	X	X	X
12. <i>Opuntia basilaris</i> Engelm. & Bigel.....	X	X sp.	X sp.
13. <i>Opuntia acanthocarpa</i> Engelm. & Bigel...	X	?	?
14. <i>Physalis crassifolia</i> Benth.....	X	X sp.
15. <i>Prunus fasciculata</i> Torr.....	?	X sp.
16. <i>Fraxinus</i>	X	X sp.	X sp.
17. <i>Populus</i>	X	X sp.	X sp.

In the above table the interrogation point (?) is used to indicate that while the genus or species may well occur it has not been specifically identified. The abbreviation sp. following the sign indicating the presence of a plant in the dung denotes that characteristics typical of the genus occur but that the species could not be positively determined.



Rampart Cave, Arizona. Position of entrance is shown by the arrow. The clumps of tall, narrow, loosely branching shrubbery in the foreground are *Fouquieria*. Hulbert Burroughs, photographer.



A. Trail to Muav Cave from Lake Mead. The picture shows the relative abundance of vegetation. Hulbert Burroughs, photographer.



B. Undisturbed layer of sloth dung in Rampart Cave. The dung layer at this point comes to within an approximate distance of four feet from the ceiling. Hulbert Burroughs, photographer.



Nothrotherium shastense Sinclair

Typical dung ball showing preservation of fibrous material. Nat. size. Specimen in the vertebrate palæontological collections of the California Institute of Technology.

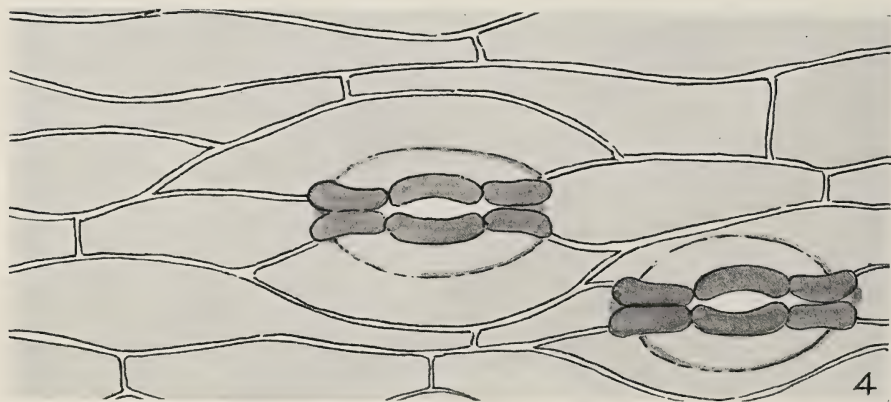
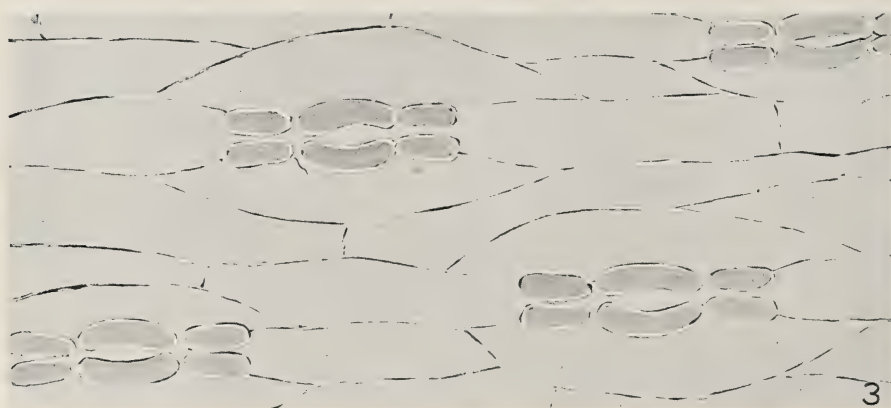
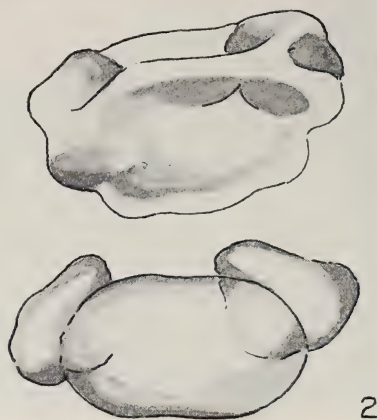
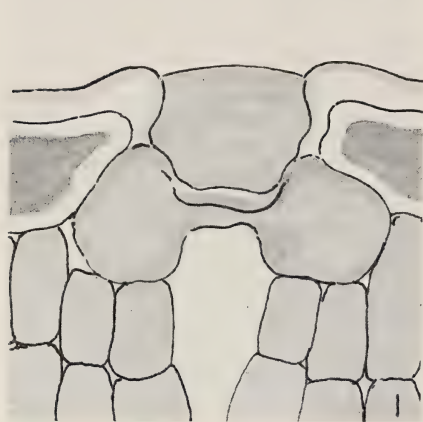
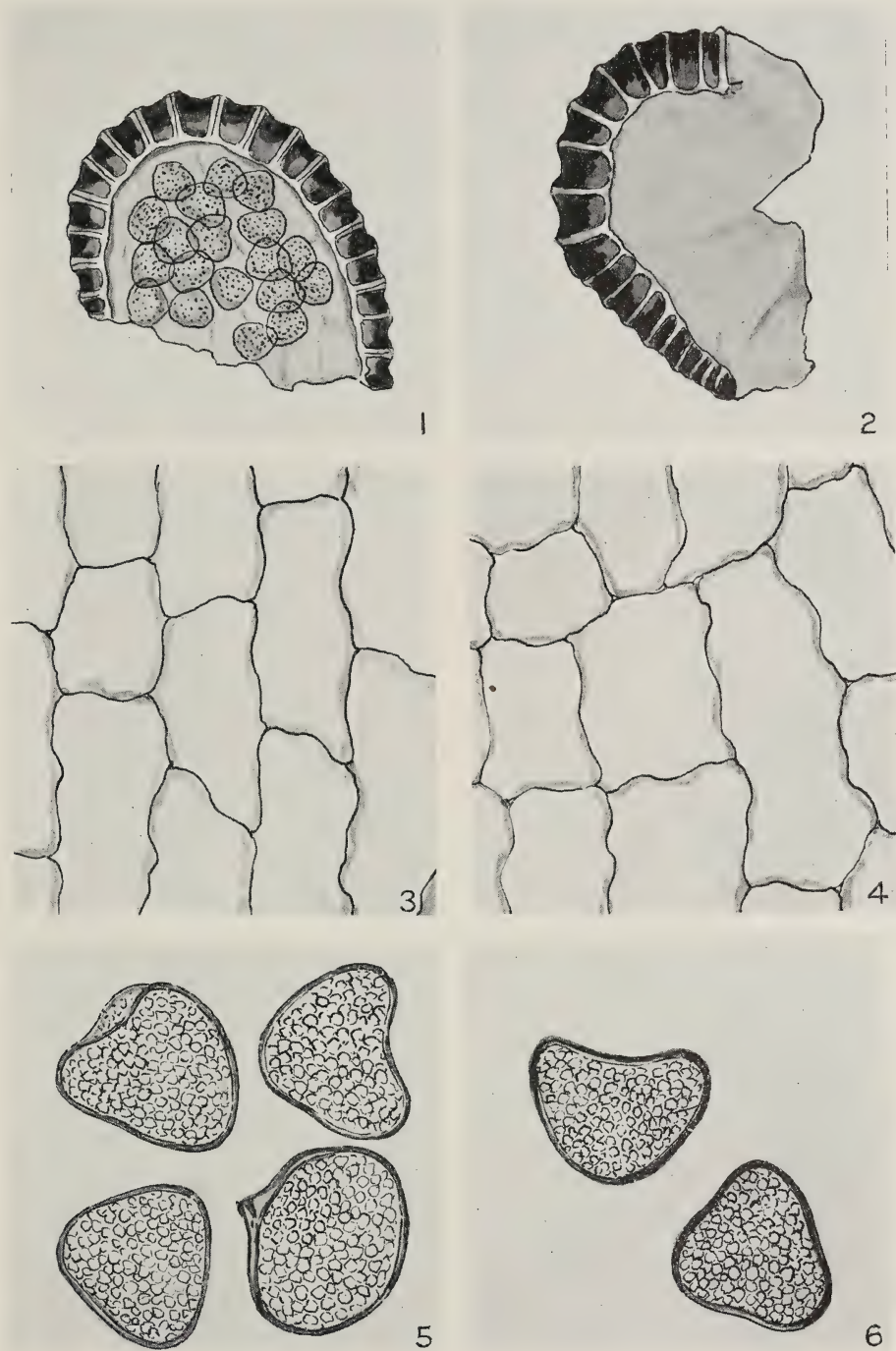


FIG. 1—*Ephedra nevadensis* Wats. Longitudinal section through a stomate; $\times 300$.
 FIG. 2—*Ephedra*. Isolated guard cells from sloth dung; $\times 300$.
 FIG. 3—*Ephedra*. First sub-surface view of epidermis from sloth dung; $\times 300$.
 FIG. 4—*Ephedra*. First sub-surface view of epidermis of type section; $\times 300$.



Adiantum Capillus-Veneris L.

- FIG. 1—*Adiantum*. Sporangium with spores in situ, type section; $\times 75$.
 FIG. 2—*Adiantum*. Sporangium, from dung; $\times 75$.
 FIG. 3—*Adiantum*. Epidermal cells from leaf, type section; $\times 300$.
 FIG. 4—*Adiantum*. Epidermal cells from leaf, from dung; $\times 300$.
 FIG. 5—*Adiantum*. Spores, type slide; $\times 300$.
 FIG. 6—*Adiantum*. Spores, from dung; $\times 300$.

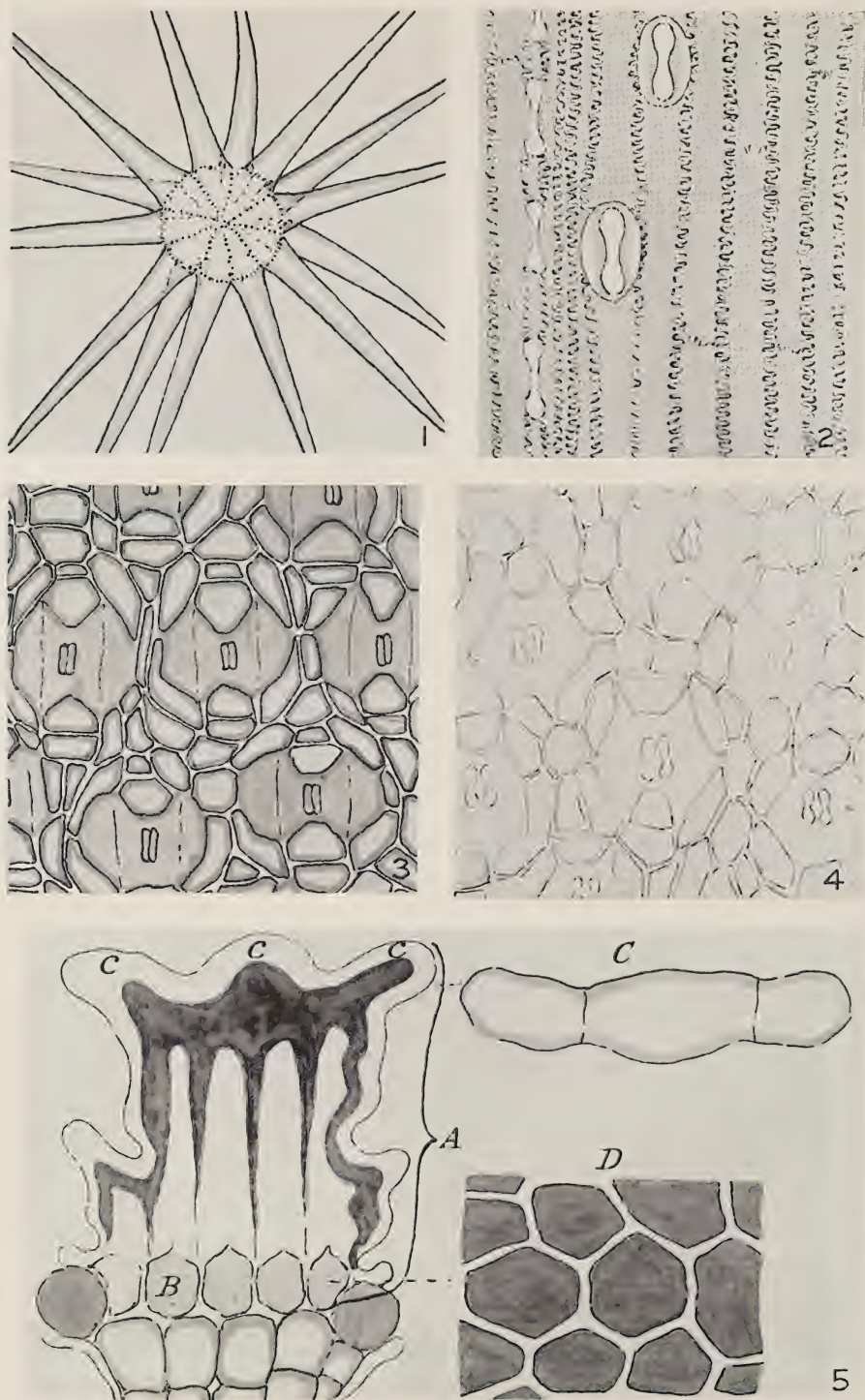


FIG. 1—*Sphaeralcea ambigua* Gray. Stellate hair from leaf or stem, from dung; $\times 75$.
 FIG. 2—*Aristida* sp. Epidermal cells with stomates, from dung; $\times 300$.
 FIG. 3—*Yucca mohavensis* Sarg. First sub-surface view of epidermis with cells and stomates, type section; $\times 300$.
 FIG. 4—*Yucca mohavensis* Sarg. Epidermis with cells and stomates from dung; $\times 300$.
 FIG. 5—*Yucca mohavensis* Sarg. Transverse section through five cells of the epidermis. At A are shown the cells composing the epidermis proper. At B, cells of reticulated layer. At C, surface view of cells CCC. At D, cells of reticulated layer, horizontal optical section of cells B. Type section; $\times 300$.

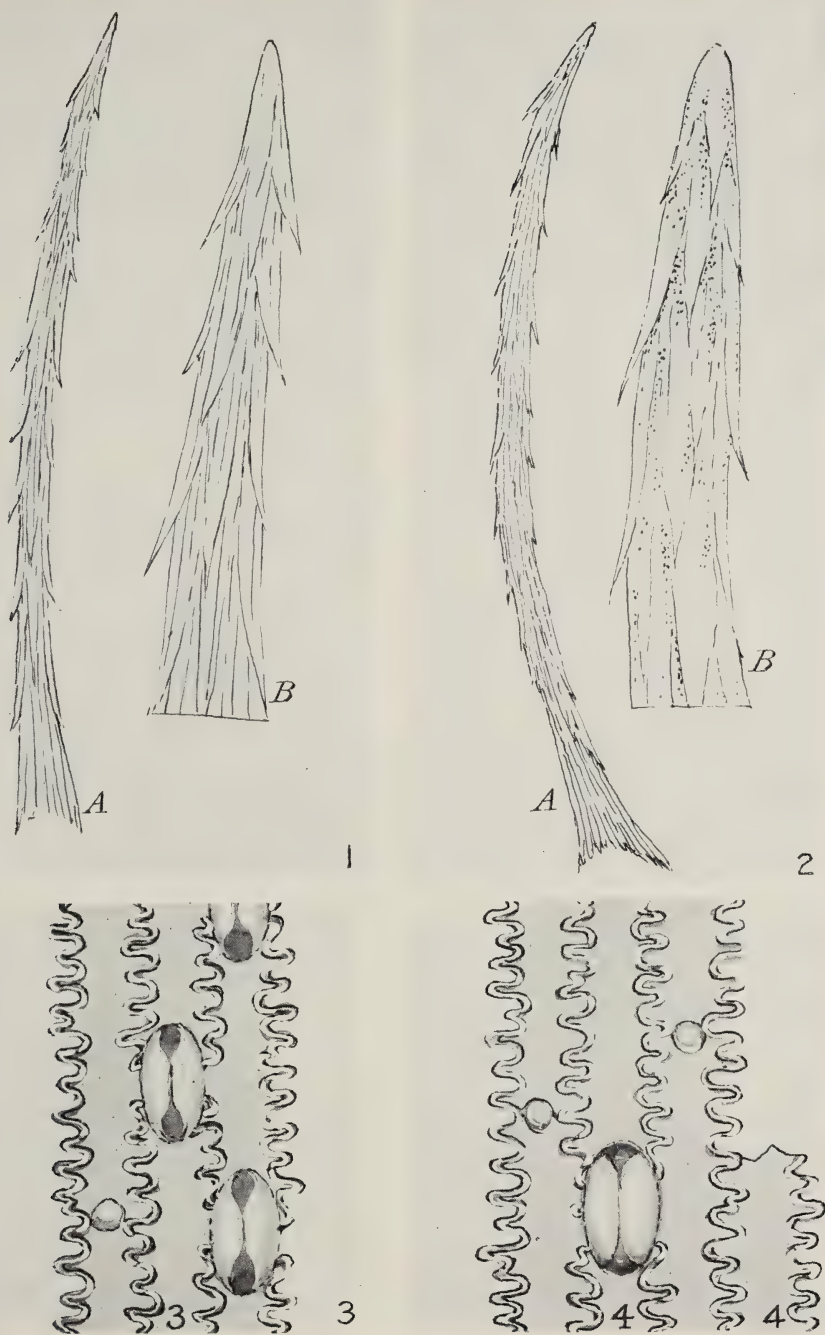


FIG. 1—*Opuntia basilaris* Engelm. & Bigel. A—spine; $\times 75$. B—tip of spine; $\times 300$. Type material.

FIG. 2—*Opuntia* sp. A—spine; $\times 75$. B—tip of spine; $\times 300$. From dung.

FIG. 3—*Phragmites communis* Trin. Epidermal cells with stomates, type section; $\times 300$.

FIG. 4—*Phragmites communis* Trin. Epidermal cells with a single stomate; $\times 300$.

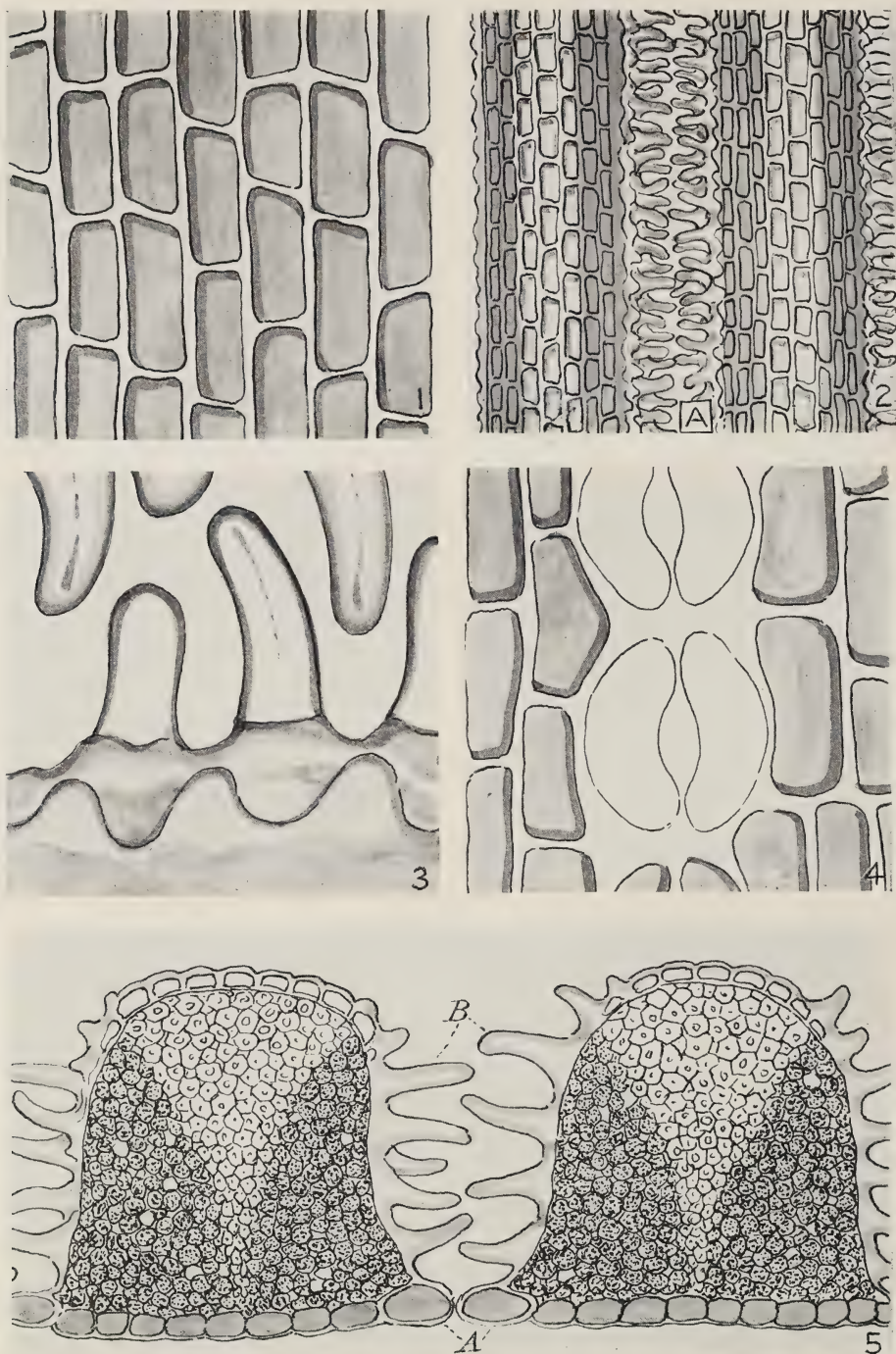


FIG. 1—*Nolina Bigelovii* (Torr.) Wats. Epidermal cells, first sub-surface view; $\times 400$.
 FIG. 2—*Nolina Bigelovii* (Torr.) Wats. Epidermis and view of rift at A, the latter lined with papillae. The stomates are visible only from the under side of the epidermis; $\times 60$.
 FIG. 3—*Nolina Bigelovii* (Torr.) Wats. Papillae; $\times 400$.
 FIG. 4—*Nolina Bigelovii* (Torr.) Wats. Stomates; $\times 400$.
 FIG. 5—*Nolina Bigelovii* (Torr.) Wats. Transverse section of leaf. Position of stoma shown at AA. Papillae lining rift at B; $\times 250$. All figures from type sections.

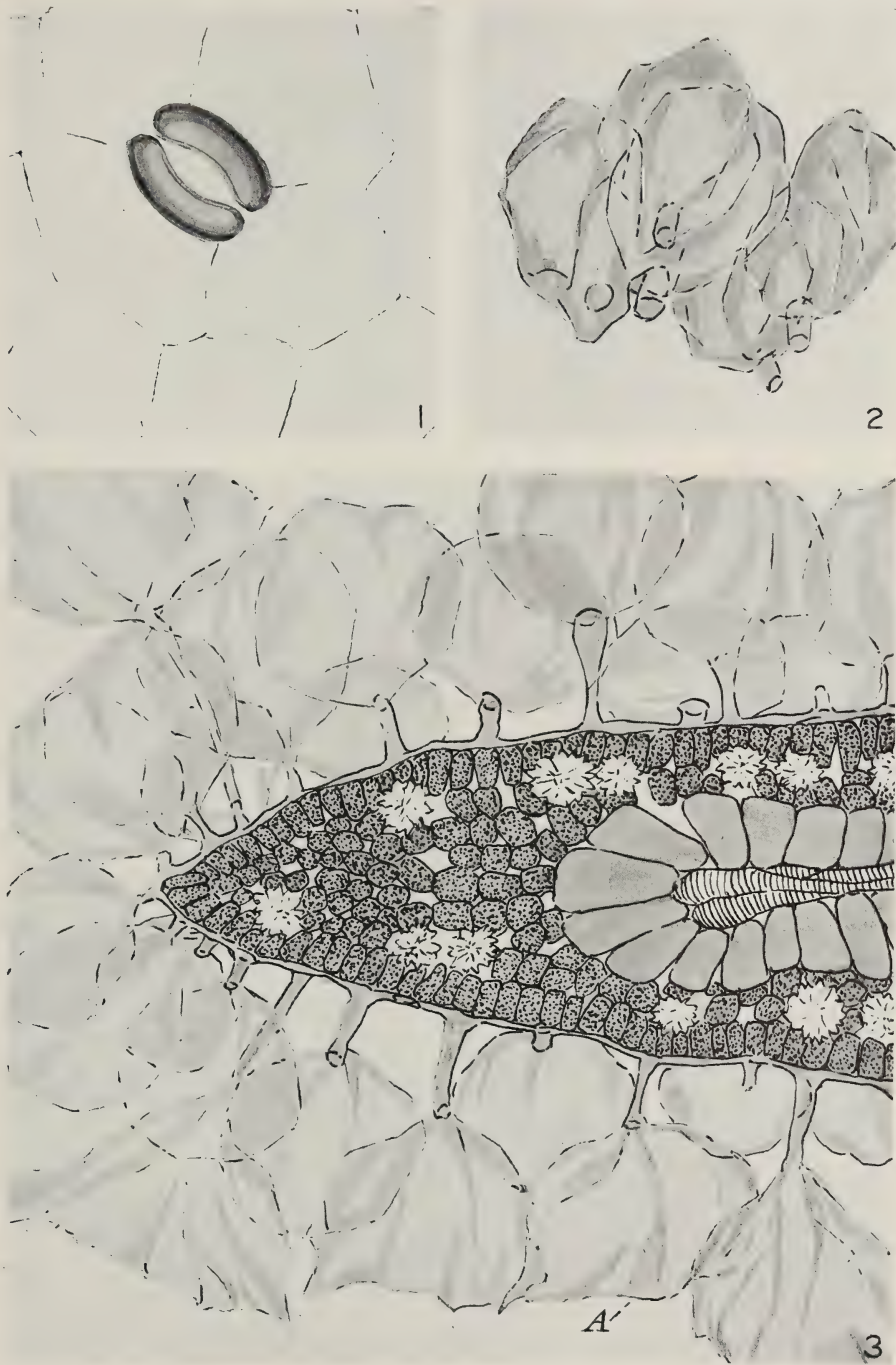


FIG. 1—*Atriplex hymenelytra* (Torr.) Wats. Epidermal cells and stomate, type section; $\times 300$.

FIG. 2—*Atriplex*. Inflated hairs, from dung; $\times 150$.

FIG. 3—*Atriplex*. Transverse section through margin of leaf showing inflated hairs in situ, type section; $\times 300$.

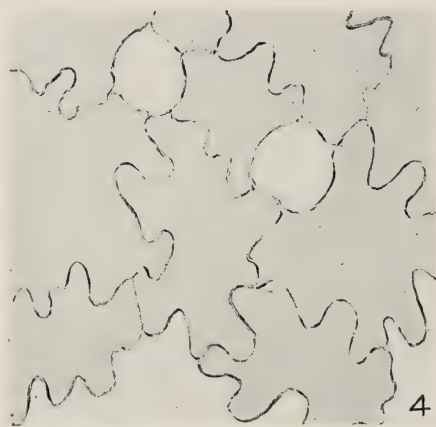
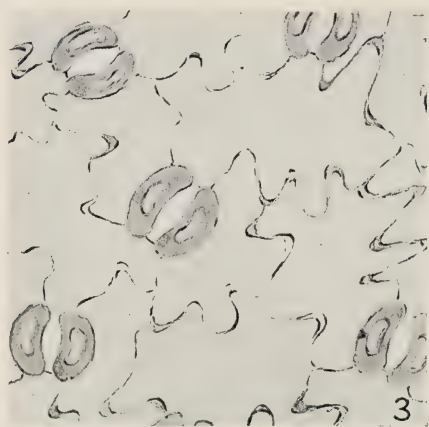
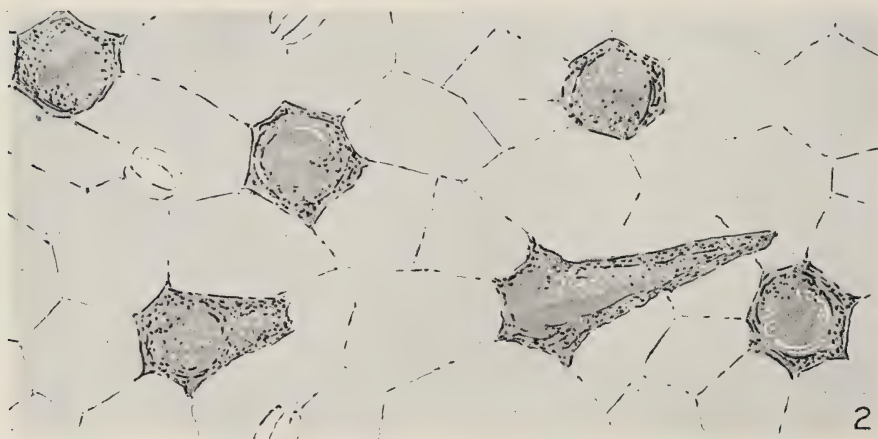
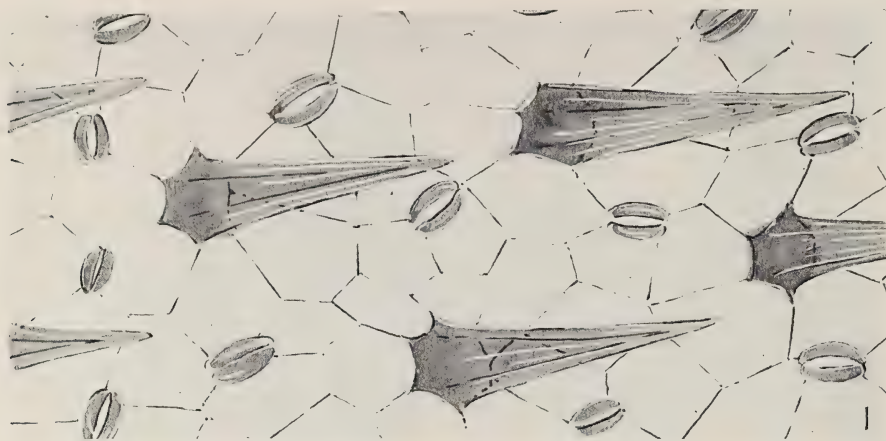


FIG. 1—*Prunus fasciculata* (Torr.) Gray. Epidermal cells and stomates. Hairs shown somewhat foreshortened. Type section; $\times 300$.
 FIG. 2—*Prunus* sp. Epidermal cells, stomates, and hairs, from dung; $\times 300$.
 FIG. 3—*Physalis hederifolia* Gray. Epidermal cells and stomates, type section; $\times 300$.
 FIG. 4—*Physalis* sp.? Epidermal cells, from dung; $\times 300$.

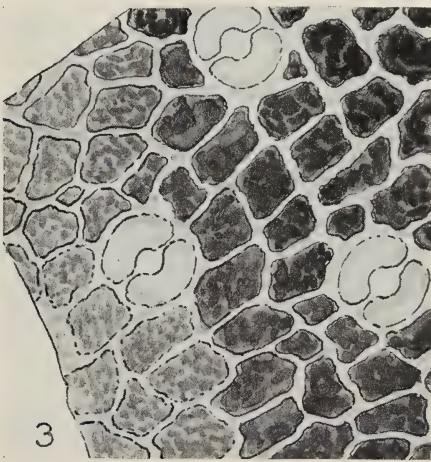
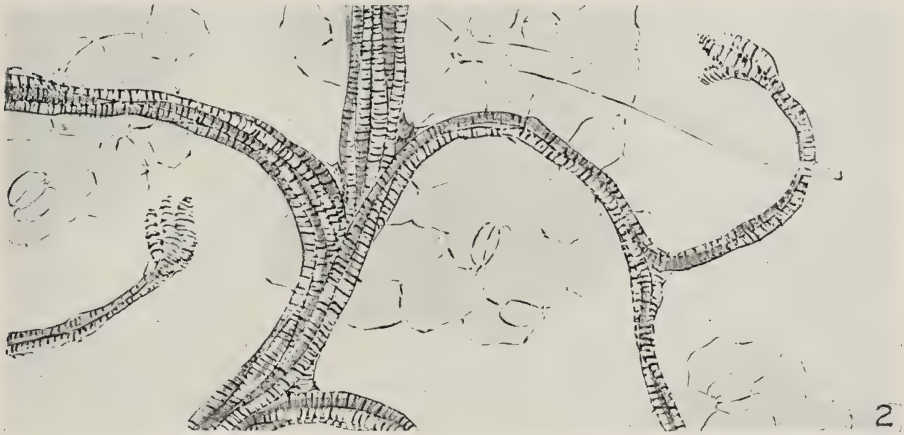
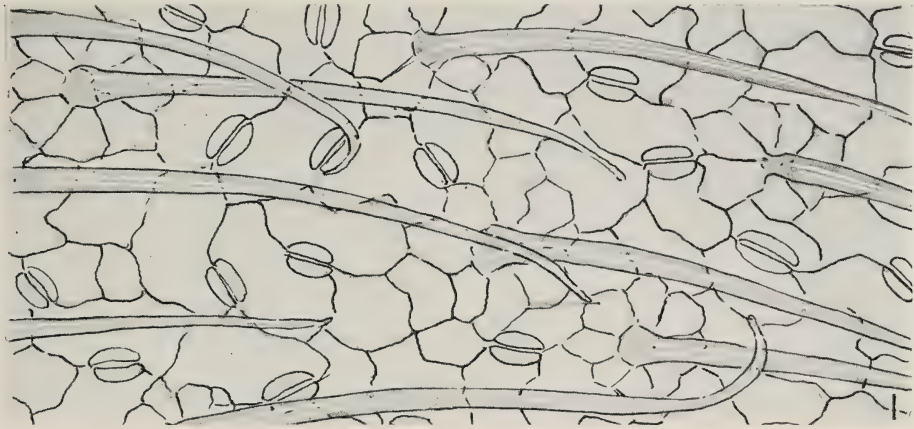


FIG. 1—*Cassia Covesii* Gray. Epidermal cells with stomates and hairs, type section; $\times 300$.
 FIG. 2—*Cassia* sp. Epidermal cells with stomates and hair. Fragments of epidermis adhering to shreds of fibro-vascular bundles. From dung; $\times 300$.
 FIG. 3—*Larrea divaricata* Cav. Epidermal cells with stomates and pigment, type section; $\times 300$.
 FIG. 4—*Larrea*. Epidermal cells and pigment, from dung; $\times 300$.

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